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Thresholds of Disturbance: Land Management Effects on Vegetation and Nitrogen Dynamics

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14. ABSTRACT
Objective 3 of FY2000 SON (CSSON-00-03) requested research to ‘determine whether there are thresholds in spatial extent, intensity or frequency above and/or below which the natural system cannot sustain identified ecological and/or land use disturbances.’ The Savannah River Ecology Laboratory (SREL) conducted a field experiment to evaluate the ecological effects of military training and forest management for longleaf pine at Fort Benning, to determine if there are thresholds beyond which upland ecosystems cannot sustain the combined effects of these land uses.

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Acronyms

ANOSTEP - stepwise analysis of dissimilarity
ANOSIM - analysis of dissimilarity
ANOVA - analysis of variance
ARA - acetylene reducing activity
C - clayey soils
C – constancy
C- carbon
DECODA – Database for Ecological Community Data
DBM – diameter at breast height
F - fidelity
F2 - accelerated (2-yr) prescribed fire treatment
F4 - delayed (4-yr) fire treatment -left unburned through the 2003 growing season
Fh - fire frequency 5-6 fires between 1986 and 2000
Fl - fire frequency 0-2 fires between 1986 and 2000
Fm - fire frequency 3-4 fires between 1986 and 2000
GIS – geographical information system
GLA – Gap Light Analyzer software
GLM – General Linear Model
H - Shannon diversity index
ISA - Indicator Species Analysis
IV - indicator value
J - Shannon evenness index
LY = loblolly pine
MANOVA – multivariate analysis of variance
MBC - soil microbial biomass carbon
Mh - heavier military use compartments open to mechanized training (tracked vehicles)
Ml - lighter use sites in compartments with dismounted infantry training (foot traffic)
N- nitrogen
NH_4 - Ammonium
NMDS - non-metric multidimensional scaling
Nmin - potential net nitrogen mineralization
NO_3 – Nitrate
PH = pine hardwoods
PPM – parts per million
PRS - Plant Root Simulator
S - sandy soils
SL = shortleaf pine
SREL – Savannah River Ecology Laboratory
SU - sampling unit
1H - 1st growing season post-fire, heavy use sites
1L - 1st growing season post-fire, light use
3H - 3rd growing season post-fire, heavy use
3L - 3rd growing season post-fire, light use

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Acknowledgements

This research was supported by DoD Strategic Environmental Research and Development Program (SERDP) CS-1302, SERDP Ecosystem Management Project (SEMP) CD-1114E-00, and the Office of Biological and Environmental Research, U.S. Department of Energy through the Financial Assistant Award no. DE-FC09-96SR18546 to the University of Georgia Research Foundation. We thank John Brent, Pete Swiderek and the staff of Fort Benning for assistance in establishing this research. Hugh Westbury, the SEMP-Ft Benning host site coordinator, has been instrumental in project operation on Fort Benning. We thank Nicole White, Maggie Johnston, Skip Kizzire, Jaclyn Schnurr, Tonya Mallin, Adam Boretsky, Meredith Tomblin, Matt Opdyke, Jason Hupp, Karen Shepherd, Rawle Hercules, T. Wayne Barger, Jerry Hairston, Phillip Duncan, Tonya Euell, Lindy Paddock, Todd LaJeunesse, Peter Hartel., Greg Brannon, Jennifer Lang, Bruce Haines and Chris Crawford for technical assistance, and Rob Addington and Hal Balbach for comments on manuscripts.

Executive Summary

Land at Fort Benning is used for multiple purposes. Use for military training ranges from light disturbance by foot and occasional light vehicle traffic to heavy disturbance by repeated armored vehicle traffic. Upland mixed pine/hardwood forests have been managed over the last 25 yr, by periodic thinning and burning, to promote longleaf pine (*Pinus palustris*) savanna for the endangered red-cockaded woodpecker (*Picoides borealis*). These military and forestry land uses occur over a heterogeneous environment. The installation's location in the Fall Line Sandhills region is an ecotone between the Piedmont and Coastal Plain provinces. Vegetation and soils are influenced by topography, drainage, periodic fires, and a long history of human use. Some combinations of land uses may not be sustainable over upland environments at Fort Benning. The ecosystem may lose nutrients or fail to regenerate desirable species. Objective 3 of FY2000 SON (CSSON-00-03) requested research to 'determine whether there are thresholds in spatial extent, intensity or frequency above and/or below which the natural system cannot sustain identified ecological and/or land use disturbances.' The Savannah River Ecology Laboratory (SREL) conducted a field experiment to evaluate the ecological effects of military training and forest management for longleaf pine at Fort Benning, to determine if there are thresholds beyond which upland ecosystems cannot sustain the combined effects of these land uses.

This research was conducted from 2000 through 2004 in 32 upland forest stands at Fort Benning. We manipulated the frequency of prescribed fire, normally at 3 yr intervals, to a) an accelerated 2-yr interval or b) a delayed 4-yr interval, and compared ecosystem responses between sites on sandy vs clayey soil and in lighter training (primarily dismounted infantry) vs heavier training (compartments open to mechanized training) area. We compared ground layer vegetation and nitrogen cycling over five years, which encompassed two 2-yr fire intervals and one 4-yr fire interval, to determine if these measures show thresholds beyond which combinations of lighter or heavier military training and shorter or longer prescribed fire interval cannot be sustained.

Longleaf pine ecosystem is the desired future condition for upland forests on appropriate sites at Fort Benning. Under the assumption that a short (2-yr) fire interval is the external force that sustains longleaf ecosystem, sandy or clay longleaf-dominated sites with lower or higher military use and in the 2-yr fire treatment provided 'control' or threshold values for transition to the longleaf ecosystem domain. We hypothesized that the more open environment generated by heavier training and frequent fire could promote regeneration of species typical of pine ecosystems, and hasten transition to a longleaf pine forest, provided species tolerate the disturbance legacy of mechanized military training. We also hypothesized that the magnitude of ecosystem response to fire and military training disturbance would be less, and the transition to pine-dominated forest faster, for sites on sandy soils because the pool of tolerant species is smaller and the successional pathway is shorter on these lower quality soils.

Baseline surveys conducted in 2000 and 2001 revealed that vegetation and soil conditions at the start of this research reflected land use and soil texture differences among the study sites:

A survey of disturbance features revealed that land use or natural disturbance features occupied from 7% to 50% of sample transect length. Clayey sites in heavy military use areas had greater length of sampling transects in disturbance features. Road-like features, including active and remnant trails, roads, and vehicle tracks or trails, were, collectively, the most frequent and abundant disturbance.

Differences in soil properties among the 32 upland forest stands were related to soil texture and military land use intensity. Results suggest organic layers in sandy compared to clayey sites could immobilize nitrogen through relatively slow rates of decomposition and nitrogen release to the mineral soil. In the mineral soil, field and laboratory results suggest that mineralization processes enhance nitrogen availability in sandy sites, especially in land compartments with heavier military training. In contrast to the sandy sites, greater organic layer mass in clayey sites, particularly in sites with lighter military use, favors faster decomposition, but the lower nitrogen availability observed in the field on the heavier use sites suggests mineralized nitrogen can be bound by fine soil particles.

Ordination, used to visualize patterns in vegetation composition, revealed a strong effect of military training on canopy and ground layer composition at the start of this research. The canopy tree ordination also reflected the proportion of pine, particularly longleaf pine. We distinguished four forest types, based on the dominant canopy trees: longleaf pine stands, shortleaf stands, mixed pine hardwood stands, and loblolly stands. Although differences were less pronounced than in the canopy, ground layer vegetation also reflected the canopy dominant. Pine-hardwood and longleaf stands had different ground layer composition. *Andropogon* sp., primarily broomsedge, *A. virginicus*, *Pityopsis*, and sweetgum (*Liquidambar*) seedlings were abundant in multiple canopy types. Pine-hardwood forests had abundant *Vitis* sp, while bracken fern (*Pteridium aquilinum*) was abundant in longleaf stands. The abundance of legumes and grasses was higher in the longleaf stands than in the other forest types. Over all forests types, 70 % pine canopy appears to be a threshold for ground layer vegetation with abundant grasses and legumes.

Vegetation analyses after two, 2-yr fire cycles and one, 4-yr cycle revealed the shorter, 2-yr fire interval caused the ground layer vegetation to become more similar to that of clayey sites with heavier military use; i.e., to be characterized by more xeric sandhills species and nonwoody legumes, graminoids, and forbs. However, comparisons of ground layer composition between longleaf stands and those of the combined other (pine-hardwood, shortleaf, loblolly) forest types revealed that sites that were initially different did not converge over time. The shorter, 2-yr fire interval did not cause initially dissimilar sites to become more similar to, or initially similar sites to diverge from, longleaf communities. Although the shorter fire interval did not cause dissimilar sites to shift to longleaf, either 1) heavier military use or shorter fire frequency in clayey sites, or 2) shorter fire frequency in sandy sites can maintain ground layer composition similar to that of longleaf sites. These results partially support our hypothesis that the magnitude of ecosystem response to fire and military training disturbance would be less, and the transition to pine-dominated forest faster, for sites on sandy soils. Shorter fire frequency alone can maintain longleaf ground layer composition on sandy sites, but both shorter fire frequency and heavier military training may be needed in clayey sites.

Within the context of Fort Benning's ecosystem management model, longer, 4-yr fire intervals in sandy sites or the combination of longer fire interval and lighter military use in clayey sites may cause sites to move away from the longleaf domain and lengthen the successional trajectory. In contrast, a 2-yr fire interval and heavier military use in clayey sites or the 2-yr fire interval in sandy sites may maintain sites within the desired longleaf understory domain. However, in sampled stands the more frequent burning did not result in high levels of legume abundance and associated N inputs, which could offset nitrogen losses due to fire. Further, more frequent burning did not promote longleaf regeneration sufficient to hasten transition to a longleaf pine forest. Longleaf regeneration was absent to low over all sites. Over half (57 %) of marked pine seedlings (all species combined) died between 2001 and 2002; mortality was higher in longleaf stands and 2-yr fire frequency. Thus, despite promoting desirable understory composition, more frequent fire may inhibit regeneration. These results only partially support out hypothesis that the more open environment generated by heavier training and frequent fire could promote regeneration of species typical of pine ecosystems, and hasten transition to a longleaf pine forest. If seedling establishment limitation is overcome, e.g., by planting, management that maintains a relatively open canopy (prescribed fire, thinning) and low soil disturbance (lighter compared to heavier military training), can promote growth into grass, rocket, and sapling stages. In summer, 2004, after all sites were burned following both 2-yr fire intervals and one 4-yr fire interval, the number of grass stage individuals in a stand increased with the number of historical fires (1980-2000), longer time since fire, and the percent of sand in the soil; the number of rocket stage individuals increased with increasing number of historical fires. These conditions were common in longleaf and shortleaf stands that had experienced higher fire frequency and forest management for an open canopy, but lighter military use.

In summary, military training and frequent fire have, over the longer term (decades), interacted with soil texture to influence forest canopy and ground layer composition, and soil conditions, at Fort Benning. Over the shorter term of our research (four years), frequent fire (on sandy sites), or frequent fire combined with heavier military use (on clayey sites) can cause convergence toward 'sandhills' ground layer vegetation dominated by more xeric species, graminoids, and legumes, but these land uses are not sufficient to cause initially dissimilar sites to shift (cross a threshold) to longleaf pine understory. Management to restore longleaf pine forests must overcome recruitment limitations and may be inhibited by frequent fire; recruitment of longleaf was nonexistent to low over all sites and seedlings/sprouts of all species were reduced by prescribed fire. If recruitment limitation is overcome, management that maintains a relatively open canopy and low soil disturbance can promote longleaf pine growth into grass, rocket, and sapling stages and may facilitate restoration of longleaf pine ecosystem as conceptualized in the Fort Benning ecological restoration model.

Objective

Land use for military training at Fort Benning ranges from light disturbance by foot and occasional light vehicle traffic to heavy disturbance by repeated armored vehicle traffic. Upland mixed pine/hardwood forests are thinned and periodically burned to promote longleaf pine (*Pinus palustris*) savanna for the endangered red-cockaded woodpecker (*Picoides borealis*). Some combinations of these land uses may not be sustainable. The ecosystem may lose nutrients or fail to regenerate desirable species. Objective 3 of FY2000 SON (CSSON-00-03) requested research at Fort Benning to 'determine whether there are thresholds in spatial extent, intensity or frequency above and/or below which the natural system cannot sustain identified ecological and/or land use disturbances.'

SREL's research examined thresholds related to military training and forest management, principally through aggressive use of prescribed fire, at Fort Benning. The broad objective was *to evaluate the ecological effects of military training and forest management for longleaf pine, to determine if there are thresholds beyond which upland ecosystems cannot sustain the combined effects of these land uses*. We tested the hypothesis that underlying soil type (texture), which partly determines soil nutrient cycling as well as forest composition and dynamics, modifies the effects of military training and forest management, and influences thresholds for sustainability.

This research was conducted in 32 upland forest stands at Fort Benning. We manipulated the frequency of prescribed fire, which has been applied at roughly 3 yr intervals since 1980, to a) an accelerated 2-yr interval or b) a delayed 4-yr interval, and compared ecosystem responses between sites on sandy vs clayey soil and in lighter training (primarily dismounted infantry) vs heavier training (compartments open to mechanized training) area. We compared ground layer vegetation and nitrogen cycling over five years, which encompassed two 2-yr fire intervals and one 4-yr fire interval, to determine if these measures show thresholds beyond which combinations of military training and prescribed fire cannot be sustained.

Background

Land use at Fort Benning

Military training at Fort Benning generates disturbance. Mechanized training using tracked and wheeled vehicles compacts soil and crushes or uproots vegetation (Demarais et al. 1999) at localized scales in compartments open to this training at Fort Benning. At broader spatial scales, dismounted infantry training can result in vegetation being cut or trampled (Demarais et al. 1999). Disturbances from these military activities also can be cumulative, especially if the same training sites are used repeatedly (Demarais et al. 1999). Frequent or severe training can result in soil compaction and vegetation loss or retrogression to early or midsuccessional communities (Demarais et al. 1999).

Forest management practices at Fort Benning also generate disturbance and can impact soil processes as well as vegetation. Upland forests at Fort Benning are managed, primarily through thinning at 9 – 10 year intervals and burning at roughly three-year intervals, to discourage hardwoods and encourage longleaf pine (*Pinus palustris* Miller) regeneration and longleaf ecosystem maintenance as habitat for the endangered red-cockaded woodpecker (*Picoides borealis* Vieillot) on appropriate sites (Fort Benning 2002). Skidders used during forest harvests can compact soil and crush or destroy vegetation. Fire in southeastern forests maintains an open overstory, can cause an increase in overland water flow and soil erosion due to combustion of vegetation and the forest floor, and can cause an immediate increase in soil nutrients, including nitrogen (Schoch and Binkley 1986; Beckage and Stout 2000; Wan et al. 2001; Caldwell et al. 2002).

Land use at Fort Benning occurs over a heterogeneous environment. The installation's location in the Fall Line Sandhills region is an ecotone between the Piedmont and Coastal Plain provinces. Vegetation of the Fall Line Sandhills region is influenced by topography, drainage, soil composition and fertility, and periodic fires (Wells and Shunk 1931; Weaver 1969; Skeen et al. 1993). The heterogeneous soils are primarily ultisols and entisols, and include Troup sandy loams, Lakeland sands, Siley loamy sands, and Nankin sandy loams (Johnson 1983). Soil properties reflect prior land use, which was mainly farming and grazing (Fort Benning 2002), and more recent military use and forestry practices.

Ecological thresholds

Ecological thresholds can identify the need for a change in land management. Thresholds have been defined as a "sudden change in any property of an ecological system as a consequence of smooth and continuous change in an independent variable" (Muradian, 2001) or a deflection of system response (or an ecological discontinuity) following a stimulus or stressor (Romme et al., 1998). Over the last few years, thresholds have become associated with management and restoration of ecosystems as 'dynamic regimes' (Mayer and Reitkerk 2004). Thresholds are associated with changes in internal relationships or external forces that shift ecosystems from within the boundary conditions of sustainability (Kaine and Tozer 2005) to alternative regimes (Scheffer and Carpenter 2003; Mayer and Reitkerk 2004).

Point (abrupt) or more gradual (zone) ecological thresholds (Huggett 2005) have been associated with natural or human-caused changes in external forces. For example, at a point threshold, habitat loss results in rapidly increased probability of population extinction (Huggett 2005). Changes in fire patterns, alone or in combination with factors, such as herbivory, that remove biomass, have been shown to exceed a threshold and cause grassland-woodland domain shifts (Li 2002; Gillson 2004). A fire return interval threshold is associated with maintenance of juniper woodlands (Fuhlendorf et al. 1996). In the southeastern US, frequent fire, which removes fire-intolerant hardwoods and woody regeneration, has been associated with a more gradual shift from hardwoods to pine-dominated forests (Heyward 1939; Quarterman and Keever 1962; Monk 1965; Brockway and Lewis 1997; Kush et al. 1999, Hedman et al. 2000, Provencher et al. 2001, Heuberger and Putz 2003 and many others).

Thresholds and forest management at Fort Benning

Longleaf pine (*Pinus palustris*)-dominated forests are the desired future domain for upland forests at Fort Benning (Fort Benning 2002). These historically more widespread forests are maintained by frequent fire. The conceptual ecological restoration model for the installation (Fig. 1; adapted from http://tnc-ecomanagement.org/images/ftbenning_models.pdf - website accessed 3/23/2005 2:20pm) utilizes prescribed fire, thinning, and other forestry techniques as 'external forces' to transition current mixed pine hardwood and pine plantations to the desired future longleaf domain. Management actions first are employed to promote longleaf pine regeneration; sites are then maintained to promote longleaf growth into the canopy (Fig. 1).

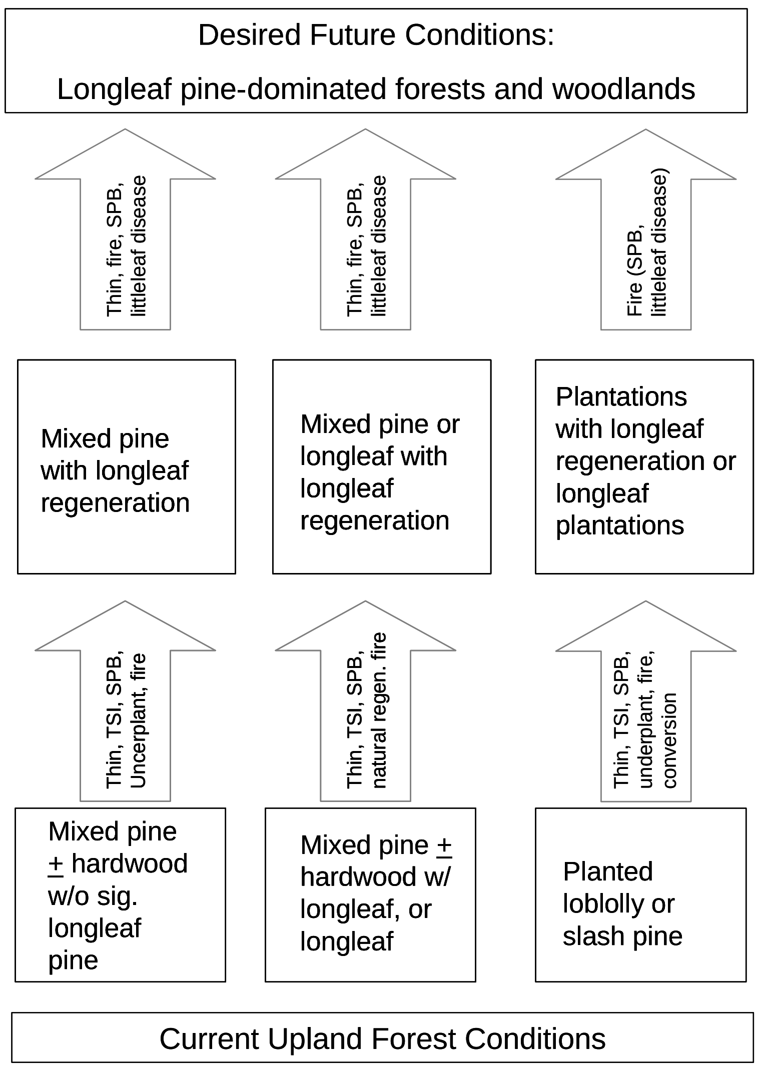


Figure 1. Ecological restoration model for Fort Benning.

Some researchers have suggested a species composition threshold or 'switch' associated with longleaf pine communities, driven by positive feedback between fire and the ratio of flammable longleaf pine litter to less flammable (hardwood) litter (Streng & Harcombe 1982, Wilson & Agnew 1992, Liu et al. 1997). SREL research examined ground layer vegetation, including tree regeneration, and nitrogen cycling responses to determine if accelerating or delaying prescribed fire in upland forest stands representing a range of current vegetation composition from mixed pine/hardwood to longleaf-dominated stands a) accelerates the transition to longleaf forest (i.e., increases pine regeneration, longleaf ecosystem species composition, or nitrogen cycling characteristics), b) retards this transition and maintains the current forest, or c) initiates a transition to a different domain (i.e, regeneration and nitrogen cycling do not reflect either current composition or longleaf pine ecosystem).

Upland forests at Fort Benning are managed over a range of military training, from 'lighter' primarily dismounted infantry training to 'heavier' mechanized training using tracked or wheeled vehicles. Examining forest ground layer and nitrogen cycling response to shorter or longer prescribed fire interval can reveal combinations of fire frequency and military training intensity and accelerate (cross a threshold) or inhibit transition to longleaf pine forest, or move the system to a different domain. We hypothesized that the more open environment generated by heavier training and frequent fire could promote regeneration of species typical of pine ecosystems, and hasten transition to a longleaf pine forest, provided species tolerate the disturbance legacy of mechanized military training.

Forest management and military training at Fort Benning also occur over heterogeneous soil types and textures (Fort Benning 2002). The majority of Fort Benning's soils are considered highly erodible (Ft Benning 2002). They are primarily Ultisols and Entisols and include Troup sandy loams (siliceous, thermic Grossarenic Kandiudults), Lakeland sands (thermic, coated Typic Quartzipsamments), Ailey loamy sand (loamy, siliceous, thermic Arenic Kanhapludults), and Nankin sandy loams (clayey, kaolinitic, thermic Typic Kanhapludults) (Johnson 1983).

Greater plant species richness can be associated with finer-textured soils in southeastern forests (Rodgers and Provencher 1999), and could reflect better soil quality, i.e., lower nutrient and water stress, or a more diverse or longer successional pathway on clayey sites. We hypothesized that the magnitude of ecosystem response to fire and military training disturbance would be less, and the transition to pine-dominated forest faster, for sites on sandy soils because the pool of tolerant species is smaller and the successional pathway is shorter on these lower quality soils.

Materials and Methods

Site selection and research design

In spring, 2000, we chose 32 sites from a set of 'typical' upland forest stands that had been prescribe-burned during the preceding winter-early spring. Half (16) the sites were on sandy (S) soil; half were on clayey (C) soil, as determined from soil survey maps for Fort Benning (Fort Benning 2002). Half the sites were in heavier (Mh) military use compartments open to mechanized training (tracked vehicles); half were lighter (Ml) use sites in compartments with dismounted infantry training (foot traffic). This design yielded eight sites within each military training x soil texture combination. We then assigned half (4) of the sites in each military training x soil texture combination to an accelerated (2-yr) prescribed fire treatment (F2), to be winter-burned in 2002. The other half of the sites was assigned to a delayed (4-yr) fire treatment (F4), to be left unburned through the 2003 growing season. Figure 2 shows the experimental design.

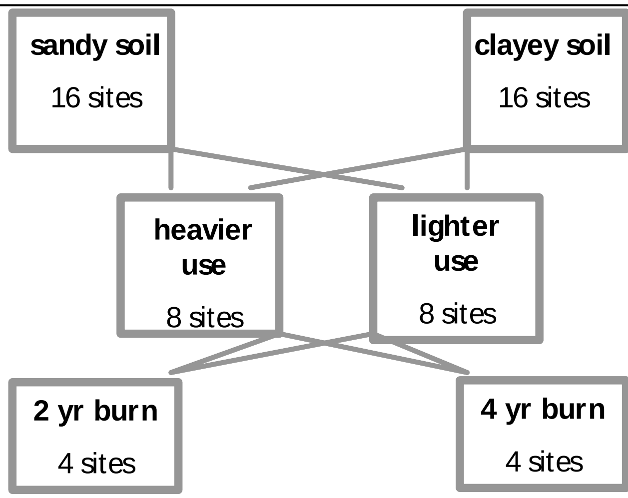


Figure 2. Experimental design.

Each site was delimited as a 400 m x 400 m area, within which we established a 100 m x 100 m sampling plot. Five 100 m transects were established at 20 m intervals within the plot, and sampling points were established at 20 m intervals on each transect, to yield 5 points per transect and 25 points in each site. We sampled vegetation and nitrogen cycling in each site from summer 2000 through summer 2004, through one 4-yr fire cycle and two 2-yr fire cycles.

Baseline surveys

Land use effects on forest composition, nutrient cycling, and dynamics are cumulative; military training, forest management, and other land use history have influenced each of the 32 upland forest sites. To compare forest response to the accelerated or delayed fire treatment between military training and soil texture categories, we first needed to determine the initial conditions in each site that have resulted from is land use history. During summer, 2000, we surveyed vegetation, soils, and 'disturbance features to determine baseline conditions and ensure that each site was correctly categorized with respect to soil texture and intensity of military use.

- Trees were surveyed at each of the 25 sampling points in each site using the point quarter method. Ground layer vegetation, defined as vegetation < 1.4 m height, was surveyed by line-intercept along a 6 m transect at each sampling point. Vegetation that intercepted the vertical plane of the transect was included.

- Surface soil texture of each site was determined from soil core samples 2 cm wide by 28 cm deep. Cores were taken from nine uniformly spaced points in each of the 32 sites and texture was determined using a micropipette method (Miller and Miller 1987).
- Land-use intensity in each site was assessed by a disturbance survey. Two 300 m transects that bisected the center of the vegetation plot were established in each 400 m x 400 m site. The transects ran North-South and East-West from the plot centers. Features associated with forestry, military use, and natural disturbance, including roads, tank trails, gullies, and canopy openings, were assessed by line-intercept along each transect.

Preliminary analyses of the 2000 survey data revealed some sites were misclassified or did not fit within the soil texture/military use categories. Consequently, two sites were dropped and two new sites added. In summer, 2001, baseline surveys were conducted in the new sites. Additional measures were taken to assess initial (pre-fire) conditions among all sites:

- Canopy openness at ground cover height was determined in 2001 above the 25 points in each 100 x 100 m plot with hemispherical photography (GLA, Frazer & Canham 1999) using a Nikon Coolpix® 950 with a FC-E8 fisheye lens converter.
- Depth of the soil A layer was measured at each sampling point in each site.

Ecosystem response measures

To compare vegetation and nitrogen cycling response to the accelerated or delayed prescribed fire treatment among soil texture and military training categories, we sampled ground layer vegetation, canopy composition, potential mineral soil nitrogen availability, soil organic layer mass and nitrogen content, litter fall, *in situ* soil respiration, litter and root decomposition from summer, 2000, through summer, 2004.

- Vegetation sampling: Ground layer vegetation was surveyed yearly by line intercept at each sampling point in each site. In 2001, we also conducted a survey of woody regeneration in each site. We added a 10 meter long x 1 meter wide belt transect perpendicular to the 6 meter ground layer transect at each of the 25 sampling points in each site. All woody seedlings and sprouts (< 30 cm tall) were identified, to species if possible, and counted. Up to 10 individuals of pine and oak species were marked in each transect. We resurveyed the transects in 2002 to determine the fate of the marked seedlings/sprouts and census new or surviving individuals.
- Regeneration: Longleaf regeneration was surveyed in each site in summer, 2004. A 2 m x 20 m belt transect was established at each of 24 points in each site. Longleaf germinants (pre-grass stage), grass-stage, rocket-stage, and saplings (> 2 m tall, < 10 cm dbh) were tallied in each transect.
- O- Layer Mass, Carbon and Nitrogen: The organic layer was collected in 32 forest stands in May 2001. We harvested 495 cm2 samples of pooled Oi, Oe, and Oa layers at eight randomly chosen locations in each stand. Samples were returned to the laboratory, where they were dried at 70 ^{o}C and weighed. Samples were then ground in a Thomas Scientific Wiley mill (Philadelphia, Pa.). Ash content was determined for 2 g of ground sample, which was then oven-dried (70 ^{o}C, 24 hr), weighed, and heated in a crucible for 4 hours at 500 ^{o}C. Mass data presented here are ash free dry mass. A subsample of each sample

was further ground in a SPEX CertiPrep 5100 ball mill (Metuchen, N.J.) and C and N were determined using a Carlo-Erba NA1500 Analyzer (Milan, Italy).

- Mineral Soil Bulk Density, Carbon and Nitrogen: A hammer corer (AMS, American Falls, ID) was used to extract soil cores (15 cm deep by 5 cm diameter) beneath each organic layer sample. The cores were stored at 5 ^{o}C in the laboratory until processing for nitrogen availability. A subsample of mineral soil used for the potential net nitrogen mineralization analysis was ground in a SPEX CertiPrep 5100 ball mill (Metuchen, N.J.) and soil carbon and nitrogen concentrations were determined using a LECO CN-2000 (LECO Corporation, St. Joseph, MI). Bulk density was calculated using the oven-dried mass of a soil core. Bulk density data was collecting in 2002 and was assumed to be representative of 2001 values. Mineral soil nitrogen and carbon pools were calculated using concentration and bulk density data.
- Potential Soil Nitrogen Availability: A hammer corer (AMS, American Falls, ID) was used to extract soil cores (15 cm deep by 5 cm diameter) beneath each organic layer sample. The cores were stored at 5 ^{o}C in the laboratory until processing for nitrogen availability. In the laboratory, four cores per plot were passed through a 6.3 mm sieve; roots were sorted and removed from the soil. A subsample of the sieved soil (ca. 10 g) was extracted using 2 M KCl (10 ml soln:1 g soil). The solution was shaken mechanically for two hours and allowed to clear overnight at 4 ^{o}C. The clear extract was pipetted off for NO_3-N and NH_4-N analysis as described below.

  The remaining sieved soil was incubated in the dark at room temperature (21 ^{o}C) in 800 ml jars to measure potential net nitrogen mineralization (Nmin) and nitrification (Hart et al. 1994). Lids were removed briefly once a week to keep the incubations aerobic. After 42 days, a 10 g soil sample was removed, extracted as described above, and analyzed for NH_4-N and NO_3-N using automated colorimetry (Alpkem FS3000, OI Analytical, College Station, Texas, RFA method number A303-S170-21 rev. B. Nitrite/Nitrate, RFA method number A303-S071-00 rev. B NH_4N) with a detection limit of 0.01 ppm. These second extracts were compared to the first to determine production of NH_4-N and NO_3-N. A final extraction was performed after 84 days to check for a delay for nitrification. Net nitrogen mineralization, net nitrification, and relative nitrification were calculated using the equations of Robertson et al. (1999): $N_{mineralized} = [(Nitrate_f + Ammonium_f)-(Nitrate_0 + Ammonium_0)]$, $N_{nitrified} = (Nitrate_f – Nitrate_0)$, and percent relative nitrification = $100 \times N_{nitrified}/N_{mineralized}$.

In addition to assessing vegetation and soil nitrogen cycling responses, we conducted a number of less extensive investigations of ecosystem conditions and responses to the land use treatments:

- Short-term fire effects: We examined the ‘short term’ (one-month) effects of fire in 15 of the stands that were burned as part of the 2-yr fire treatment in early (1/11 – 4/17) 2002. Immediate access to the stands prior to and after burning varied due to military training and burning schedules. We assessed fire effects in 5-9 stands that were accessible during a maximum one-month window before and after the fire.
  - Immediate soil temperature response to the prescribed fires was recorded by three Dallas Semiconductor integrated ibutton® temperature sensor and data loggers placed one cm deep in mineral soil at three randomly chosen locations within

each stand. Temperature loggers were placed in the stand either the evening before, or early on the morning of, the prescribed burn. Temperature (± 1 ^oC) was logged every minute during the fire. The sensors were retrieved and downloaded either later on the day of the fire, or on the following morning. Sensors were successfully deployed and retrieved in five stands.

  - The organic layer was sampled in six stands immediately before and after the prescribed fire and in 15 stands the growing season prior to (2001) and after (2002) the prescribed fire. We harvested two 494.79 cm^2 samples of pooled Oi, Oe, and Oa layers at four randomly chosen locations in each stand. Samples were returned to the lab, where they were sorted, dried at 70 ^oC for 48 hours, and weighed.
  - A soil corer was used to extract two intact soil cores (15 cm deep by 2 cm diameter) beneath each organic layer sample. The cores were stored at 5 ^oC until processing. In the laboratory, the contents of one of each pair of cores were passed through a ¼ in sieve; roots were sorted and removed from the soil. A subsample of the sieved soil (ca. 10 g) was extracted using 2 M KCl (10 ml soln:1 g soil). The solution was shaken mechanically for two hours and allowed to clear overnight at 4 ^oC. The clear extract was pipetted off for NO_3-N and NH_4-N analysis using automated colorimetry (Alpkem FS3000) with a detection limit of 0.01 ppm. The extract was also analyzed for Al and Ca using ICP-MS. A subsample of (A layer) soil was dried, ground in a Spex ball mill, and %N and $\delta^{15}N$ were determined using a Carlo Erba elemental analyzer (NA 1500) coupled to a continuous flow isotope ratio mass spectrometer (Finnigan Delta + XL). Additional 2001 and 2002 growing season NO_3-N + NH_4-N mineral soil analysis was done for all 15 stands burned for this study.

- Soil respiration (CO_2 efflux): Soil respiration measurements began in 2001 on two stands (one with sandy soil and one with clayey soil); in 2003 sampling was expanded to eight stands. To assess their influences on soil CO_2 efflux, a root exclusion treatment (2002 and 2003) was installed within each stand. To identify additional physical and biotic influences on soil CO_2 efflux, we also measured soil moisture, soil temperature, fine root production, microbial biomass carbon, tree density, and pooled organic layer mass in each site.
  - Soil CO_2 efflux was measured with a LI-COR 6200 coupled to a LI-COR 6000-09 chamber. Measurements were made using permanently installed collars, 10 cm in diameter and 5 cm long, inserted 2 cm into the mineral soil. The collars allowed repeated measurements and minimized disturbance during sampling. Measurements were made by drawing down the CO_2 concentration and measuring the flux rate as it rose from 10 ppm below to 10 ppm above ambient CO_2 concentration (as measured 10 cm above the soil surface). We used concentration change rather than a time interval for flux measurements to improve measurements on different soil types (R. Garcia, personal communication, 2001). Soil CO_2 efflux sampling was not performed on days following a rain event. We wished to avoid the possibility of suppressed measurements on the fine textured soils; these can occur when saturated soil pore space inhibits CO_2 diffusion. We also wished to avoid the potential CO_2 pulse commonly observed following the

rewetting of a dry soil (Fierer and Schimel 2003). The post rainfall alteration of soil CO_2 efflux has been identified in many studies (Lee et al. 2002, Rey et al. 2002). Given the hypothesis of soil texture influence in this study, we delayed sampling for at least 24 hr to avoid these potentially confounding sample periods.

- A trenching treatment was begun in 2002 using nine deeper (10cm) rings, installed to sever and temporarily exclude the surface component of fine roots from the soil CO_2 efflux measurement. This root exclusion treatment was installed first in the two initial sites in late January 2002, and implemented on the remaining six sites in January 2003. Care was taken to delay initial sampling until 45 days after installation due to the potential pulse of CO_2 associated with the trenching (Hanson et al. 2000). Previous studies (eg. Edwards and Norby 1999) have shown roots will circumvent exclusion barriers over time; thus, the effects of the root exclusion treatment were temporary and we include only data collected within 12 months following the treatment. Component equations for root exclusion (2002 and 2003) treatments are as follows:
- $R_r = R_{ts} - R_{nr}$ where R_{ts}= total soil CO_2 efflux rate, R_{nr}= soil CO_2 efflux rate for root exclusion treatment, R_r = root CO_2 efflux rate.
- Soil temperature was measured concurrently with soil CO_2 efflux using an Omega Engineering (Stamford, CT) (chromel/constantan) thermocouple at 10cm depth. Soil moisture at 0-6 cm depth also was measured concurrently with soil CO_2 efflux using a Theta Probe, (Type ML2x, Delta-T Devices Ltd, Cambridge, U.K.) inserted adjacent to the soil ring. Due to the lack of equipment, soil moisture was not
- Fine root production was measured in all eight sites from June 2002 to June 2003 using a modified root ingrowth method (Vogt and Persson 1991). Thirty ingrowth bags (18cm x 10cm, constructed of 2 mm fiberglass mesh) were installed in each site (N=8) in mid June 2002. Six bags were sampled from each site at 1, 3, 6, 9, and 12 months intervals after installation. A hammer corer (AMS, American Falls, ID) was used to extract soil cores (15.2 cm deep by 5.1 cm diameter) and the core contents were passed through a 6.3 mm sieve and all visible roots removed from the soil. The soil was then placed in root ingrowth bags approximating the dimensions of the removed soil cores. Care was taken to fill the bags to a similar bulk density as the original soil. After installation, the organic layer was replaced over the mesh bag. The ingrowth bags were removed at the end of their growth interval by cutting through the soil around the bag with a sharp knife the length of the bag. Samples were transported from the field to the laboratory and stored at 5° C until processed. The ingrowth bags were trimmed of surface roots outside the sampled bag. The bag was opened and roots were separated and washed from the soil. Only live roots were included; these were identified on the basis of intactness and pliability. Roots were dried at 70° C for 48 hrs and weighed to determine dry mass. Several points in one site were accidentally burned in Jan 2003 and were excluded from the final sampling.
- Soil microbial biomass carbon (MBC) was measured in all eight stands during the growing season in May 2003. In the accidentally burned stand, soil for MBC was taken from the unburned portion of the stand. A hammer corer (AMS, American Falls, ID) was used to extract four soil cores (15.2 cm deep by 5.1 cm diameter) beneath the organic layer at random points within each site. The cores were stored at 5 ^{o}C until they were processed for microbial biomass using the

fumigation extraction method (Vance et al. 1987). In the laboratory, the material from each core was passed through a 6.3 mm sieve; roots were sorted and removed from the soil. Four, 5 g subsamples of soil (oven-dry equivalent) were weighed, and two were placed in a desiccator along with 25ml $CHCL_3$; the remaining two were placed in a control desiccator. In both desiccators, a vacuum was achieved, and the samples were fumigated for 48 hours in the dark. The soil was then transferred to plastic bottles containing 50ml 0.5M K_2SO_4 and agitated for 30-45 minutes. They then were filtered through Whatman 42 filter paper and absorbance was measured at 280nm. Microbial carbon biomass was calculated using a modification of the method of Nunan et al. (1998) developed by J. Zak (unpublished data, 2004) including an expansion of the regression equation using a greater number of soil types.

- Legume and ground cover response to fire: We examined legume and ground cover response to fire in eight burned and eight unburned stands following the prescribed fire treatment in 2002.
    - A 100 m x 100 m plot, with five transects spaced at 20 m intervals to form a sampling grid, was established in the center of each of the 16 400 m x 400 m stands. Subplots were established at 12 randomly chosen grid intersections in each plot for the sampling described below. Sampling of ground layer vegetation was conducted in July and early August in both 2002 and 2003 because these months represent the peak biomass of herbaceous plants. To obtain estimates of ground layer biomass, a 0.64 m^2-circular vegetation plot (0.58 m^2 in 2003) was randomly placed near the center of each of the 12 subplots (12 subplots × 16 sites = 192 total vegetation plots sampled per year). Vegetation was clipped at ground level and sorted into categories (ferns, grasses, legumes, other forbs, woody plants <1 cm stem diameter at base, and standing dead biomass). In 2003, the harvested legumes were identified to the species level (nomenclature follows that of Radford et al., 1968).
    - All aboveground plant material was dried to constant mass at 60° C and weighed. In 2002, randomly chosen sub-samples of the forbs, grasses, and legumes were ground in a Wiley and Spex mill and analyzed on a Carlo Erba NA 1500 elemental analyzer for C and N content. In 2003, C and N analyses were repeated, but only for the legumes, which were analyzed by species. Carbon and N tissue concentrations (%) of forbs, grasses, and legumes were converted to stand-level biomass estimates of C and N pools (i.e., standing crop g/m^2) for these plant groups by multiplying the percent concentration by the biomass (g/m^2).
    - Belowground biomass was measured by taking a 5 cm diameter soil core to a 15 cm depth within each circular vegetation plot to represent belowground biomass at the stand-level. Roots and root nodules (on the legumes) were removed from the soil by hand and washed with water over a 2 mm sieve. Root and nodule mass were determined by drying them at 70º C for 24 hours and weighing them. Root samples were then ground and analyzed for C and N content as above.
    - In July 2003, we used the acetylene reduction method (Myrold et al., 1999) to measure N_2-fixation by herbaceous legumes from eight sites (two sites from each of the following: 2-year/clay, 2-year/sand, 4-year/clay, 4-year/sand). The three

most abundant legume species in each site at the time of assay were selected for N_2-fixation measurements. These species were *Cassia nictitans* (L.), *Desmodium marilandicum* [(L.) DC], *Desmodium paniculatum* [(L.) DC], *Desmodium viridiflorum* [(L.) DC], *Lespedeza hirta* [(L.) Hornemann], and *Tephrosia virginiana* [(L.) Persoon]. In addition to the acetylene reduction assay, aboveground, belowground, and nodule biomass were obtained to estimate ecosystem-level N_2-fixation by these herbaceous legumes.

- The acetylene reduction assays were performed from 14-18 July 2003. Ten individuals of each species were chosen at random and excavated (30 cm radius × 15 cm depth) (Hendricks and Boring, 1999). Small (~ 2.5 cm) fragments of nodulated roots were excised, placed into 10 ml glass test tubes, and capped with rubber serum stoppers. Acetylene generated from calcium carbide and stored in a gas sampling bag was injected into the test tubes (~ 10% of atmosphere) and the samples were allowed to incubate for 30 minutes. The reaction was terminated by transferring the samples to 10 ml Vacutainer tubes. Subsamples (1 ml) from the Vacutainers were analyzed on a Varian, Inc. gas chromatograph, equipped with a flame ionization detector. Operating parameters included a detector temperature of 160° C, an injector temperature of 135° C, 18 ml/min helium carrier gas flow rate, and a stainless steel column packed with Porapak N. An ethylene standard was obtained by injecting 1 ml of pure ethylene into a 1 liter Mason jar fitted with a rubber septum. The Vacutainers gave off a small amount of ethylene contamination, which was subtracted to obtain the final acetylene reducing activity (ARA; nmol $\cdot$ hr^{-1} $\cdot$ g nodule dry mass $^{-1}$).
- Following this assay, the nodules were dried at 70° C to a constant mass, and weighed. Ten additional individuals of each legume species were randomly chosen from each site and excavated for estimation of biomass. These plants were separated into above- and belowground material and nodules, dried at 70º C, and weighed. This biomass (aboveground and nodule) was used to predict the nodule biomass of legumes of the same species from the 2003 ground layer biomass harvests (circular vegetation plots) according to the following:

$$\frac{\text{Aboveground biomass per plant (g)}}{\text{Nodule biomass (g)}} = \frac{\text{Aboveground biomass (circular plots g/m}^2\text{)}}{\text{Predicted nodule biomass (circular plots g/m}^2\text{)}}$$

- Using the theoretical ratio of acetylene reduced to N_2 fixed of 3:1, an ecosystem-level contribution of N by legumes (g $\cdot$ m^{-2} $\cdot$ yr^{-1}) was estimated by multiplying the predicted nodule biomass for each species by their N_2-fixation rates (based on ARA values). An overall value for N_2-fixation was determined by using the mean ARA value of the three *Desmodium* species examined to estimate N_2-fixation rates for other *Desmodium* species found in the vegetation plots; the ARA value for *L. hirta* was used to estimate N_2-fixation rates for other *Lespedeza* species; and the ARA for *T. virginiana* was used to estimate N_2-fixation rates for other *Tephrosia* species. Finally, the mean ARA value for all six legume species examined was used to estimate stand-level N_2-fixation rates for the remaining eight legume genera found in the vegetation plots.

- Avian species as indicators of disturbance: We conducted point counts in 2002 to determine if abundance of bird species could be used to assess military training and forestry management practices. We selected eight burned and eight unburned stands, half with heavier military use and half with lighter use. These combinations of military training (H, L) and prescribed fire (sites burned in 2002 = 1st growing season post-fire, sites burned only in 2000 = 3rd growing season post-fire) produced four land management categories: 1st growing season post-fire, heavy use (1H); 1st growing season post-fire, light use (1L); 3rd growing season post-fire, heavy use (3H); and 3rd growing season post-fire, light use (3L).
    - In 2000, 25 vegetation sampling points were established in a 100 m x 100 m plot in each stand. Tree density (dbh > 10 cm) was measured in 2000 and groundlayer vegetation (< 1.4 m height) was measured in 2002 as described by Dilustro et al (2002). Sapling density was surveyed in 2000 by recording each shrub or tree sapling (> 1.4 m height, dbh 1 to 10 cm) that intercepted a 10 m transect at each sampling point. In 2001, hemispherical canopy photographs were taken at each of the vegetation sampling points in each plot using a Nikon Coolpix 950 with a FC-E8 fisheye lens converter. Gap Light Analyzer (GLA) imaging software was used with these photographs to estimate canopy cover.
    - To confirm the heavier vs. lighter military use categories correctly reflected level of disturbance, and to evaluate disturbance features that might influence avian species, we conducted a survey of disturbance features along two 300 m transects that bisected each 100 m x 100 m plot. Features associated with forestry, military use, and natural disturbance, including roads, tank trails, gullies, and canopy openings, were assessed by line-intercept along each transect.
    - The vegetation and disturbance survey results include 6 additional stands (2 additional stands in 3H and 3L land use categories and 1 additional stand in 1H and 1L categories). These stands were included because point counts had to be relocated (see next paragraph) or because at least one count from the selected stand fell within another nearby stand.
    - Point counts were conducted at the center of each 100 m x 100 m plot and 50 m from both ends of each disturbance survey transect (5 points/plot; 20 points/land use category). Because of windy conditions, only three point counts could be conducted in one 3H stand (18 points total/3H). Locations were modified if the land use category was not met (e. g. the area had not burned) or if the area did not meet the study criteria (e. g. was a hardwood slope forest). Three points were moved to the center of 100 m x 100 m plots in other nearby stands that had the same land use (included in the vegetation and disturbance survey results). Points were located at least 200 m apart and most were ≥ 250 m. We surveyed each point for 10 minutes, typically between sunrise and 10:00 h, during May 2002. Occurrence of each individual seen or heard was recorded by species in concentric distance bands of < 25 m, 25-50 m, and > 50 m. Because birds were detected most often beyond the 50 m band and sample size was small (20 points/ land use category) we did not limit our analysis to birds detected only within a fixed-radius of 50 m. An effort was made to not record individuals believed to have been recorded in other counts; however, some of the species can be heard from greater than the 250 m that typically separated our counts (e. g. northern

bobwhite and indigo bunting), likely causing some repeated counts of individuals. Ideally, sample size would have been larger; however, we needed to minimize time and personnel, we chose to use these constraints, which could likely mimic management constraints, to look at results from this level of effort.

Data analysis

This research was a factorial design with three main effects: soil texture (S,C), military use (Ml, Mh), and fire interval (F2,F4). There were four replicate sites in each land use combination.

Baseline surveys

Non-metric multidimensional scaling (NMDS; SAS 2000), based on Lance-Williams dissimilarities, was used to summarize trends in initial (2000) canopy and ground layer vegetation among sites. This method has been shown to be the most effective for summarizing vegetation data when the aim is to extract the major dimensions of community variation (Minchin 1987). It represents each sampling unit (SU) as a point in a coordinate system, such that the distances between all pairs of SU points are, as far as possible, in rank order agreement with their degree of difference in community composition. We compared stress (badness of fit) of one-, two-, and three-dimensional analyses to determine when adding dimensions did not substantially improve the fit. Analysis of variance (ANOVA) was used to determine if baseline vegetation measures, disturbance features, or soil textures differed among sites in the four surface soil texture/land-use categories: MhS, MhC, MlS, and MlC. Pairwise differences among categories were tested by bonferroni t-tests (SAS 2000).

To further determine the effects of land management activities over the 20 years prior to this research on initial vegetation composition or stand structure, we grouped sites by fire history, military training, and soil texture. Fire history of each stand since 1986 was determined from a map and GIS records provided by the Ft. Benning Land Management Branch. We totaled number of fires (prescribed and wildfires) and recorded year of the last fire (before 2000) for each stand. Stands were grouped into the two soil texture categories (sandy vs. clayey) and six fire frequency (low, medium, and high) x military use (lighter, heavier) categories (FlMl, FmMl, FhMl, FhMh, FmMh, FhMh) for analyses. Fire frequency categories were l: 0 – 2 fires, m: 3-4 fires, and h: 5-6 fires between 1986 and 2000. The soil texture categories were pooled in instances where preliminary analyses indicated no significant differences in military use and fire frequency effects between them.

Analysis of dissimilarity (ANOSIM), based on Lance-Williams dissimilarities, was used to test differences in ground layer vegetation composition among the fire frequency/military use categories (Clarke 1993; Clarke & Warwick 1994). ANOSIM is based on a statistic that measures the extent to which differences between groups are greater than differences within groups, using only the rank order of the dissimilarity values, rather than their arithmetic values.

The test statistic is computed as follows:

$$\boldsymbol{R} = \frac{\overline{\boldsymbol{R}}_b - \overline{\boldsymbol{R}}_w}{\boldsymbol{n}(\boldsymbol{n}-1)/4}$$

where $\overline{R}_b$ is the mean rank of the "between" dissimilarities (dissimilarities between two SUs that belong to different groups) and $\overline{R}_w$ is the mean rank of the "within" dissimilarities (those between pairs of SUs that are in the same group). The denominator of the expression $n(n-1)/4$ is the maximum possible value of $\overline{R}_b$ - $\overline{R}_w$ for a given number of SUs (n). Dividing by this maximum possible difference in mean ranks standardizes R so that its values range from -1 to +1. An R value of +1 indicates that all the between dissimilarities are ranked higher than all of the within dissimilarities. In this case, the data indicate that the groups are as different as they can possibly be. A value of R close to zero suggests that the groups are not different. The statistical significance of R can be tested using a random permutation procedure which simulates the null hypothesis of no real difference among the groups. Stepwise analysis of dissimilarity (ANOSTEP; P. Minchin unpubl.), based on Bray-Curtis dissimilarities, was used to identify the suite of species that contributed most to compositional differences among military use and fire frequency categories.

For analyses of baseline soil conditions, the 32 stands were grouped by two land use and soil texture classes, with sixteen stands in each category: heavier vs. lighter military use and clayey vs. sandy soil. All statistical analyses utilized SAS v. 8.01 (SAS Institute 2000). Analysis of variance (ANOVA, proc GLM) was used to test main effects of soil/land use intensity factors and potential interactions in laboratory soil incubations, organic layer mass and carbon and nitrogen content, mineral soil potential nitrogen availability, and PRS™ field incubations. Tukey multiple comparison tests were used for *a posteriori* comparisons among means.

Ecosystem response measures - vegetation

Line-intercept ground-layer vegetation data from the 25 sampling points within each site were first checked for taxonomic consistency. Taxa not fully identified to species level were either excluded from further analyses or assigned to the most likely species within the genus. In some cases, separately identified species within a genus were merged and the genus used as a taxon in subsequent analyses. Records that do not represent plant species, such as Coarse Woody Debris and all unknown or unidentified taxa were excluded from analyses.

The corrected data were captured into a DECODA database (Minchin 1998), together with a set of variables that indexed each sampling point by site, point number, sampling year, soil type (sandy or clayey), military use (light or heavy) and burning frequency (usually 2 or 4 years). The line intercept data from the 25 points in each site were averaged within each sampling year and all subsequent analyses were based on these average measures of species abundance across the entire site, rather than the point measures. Several community diversity indices were computed for each site in each sampling year, based on the average line intercept data. These were richness (total number of species present), total abundance (sum of the mean line intercept values of all species present), Shannon diversity (H) and Shannon evenness (J).

To summarize and visualize patterns of community variation in space and time, the ground-layer vegetation data were ordinated using non-metric multidimensional scaling (NMDS). The Bray-Curtis dissimilarity index (Bray and Curtis 1957), which has been recognized as one of the most effective for use with community data (Faith *et al.* 1987), was used to express community differences. Average line intercept data were standardized by species maximum (values within each species divided by the maximum value attained by that species), as recommended by Faith *et al.* (1987). Ordinations were performed with the number of dimensions ranging from 1 through 6 and, in order to avoid entrapment at local minima, 50 different random starting configurations were used. There is no statistical test for the required number of dimensions. We examined the scree plot (line graph of minimum stress versus number of dimensions) to identify the number of dimensions, *k*, at which further reductions in stress were relatively small and then examined the ordinations with both *k* and *k*+1 dimensions for interpretability. NMDS ordination was first performed on the entire set of sites sampled in five (or occasionally, four) years. Two additional ordinations were then produced using only the initial year's data (2000 or 2001) and using only the final year's data (2004). These were used as a visual display of the data used in the distance-based MANOVA analyses (see below).

We used vector fitting (Dargie 1984; Kantvilas and Minchin 1989) to look for correlations with explanatory variables in any direction across the ordinations. Algebraically, vector fitting is equivalent to multiple linear regression of the explanatory variable onto the set of ordination axes. For a given variable, such as military use, vector fitting finds the direction in which the coordinates of SUs have maximum Pearson product-moment correlation (*r*) with the values of the variable. Statistical significance of the correlation can be tested by random rearrangements of the data (Faith and Norris 1989). The null hypothesis that the variable has no real trend across the ordination is simulated by randomly permuting the values of the variable among the SUs. If the fitted explanatory variable is a binary variable representing an experimental treatment, the vector indicates the direction through the ordination space that optimally separates the levels of the treatment. Vector fitting was performed in each NMDS ordination, with vectors fitted for both the design variables and the calculated measures of community diversity.

We used Analysis of Similarities or ANOSIM (Clarke 1993) to test statistically whether there were significant differences in community composition between two or more groups of SUs. ANOSIM was used to test for community differences between levels of Soil Type, Military Use and Burn Frequency within each sampling year (2000, 2001, 2002, 2003 and 2004). Additional tests were also computed using the initial year of data for each site (these were mostly 2000, but 2001 for three of the sites). NMDS ordinations, Vector Fitting and ANOSIM tests were performed using DECODA version 3 (Minchin 1998). ANOSIM (using SAS v. 9.1) was also used to test differences in each year between the ground layers of longleaf stands and those of the other (pine-hardwood, shortleaf, loblolly) forest types in the combinations of soil texture, military use, and fire frequency. This analysis allowed us to determine if the change in prescribed fire frequency resulted in convergence or divergence with longleaf ground layer communities under different military use and soil texture combinations.

We used new "distance-based MANOVA" methods to assess statistical significance of main effects and interactions. These new, parametric methods allow the use of appropriate dissimilarity measures for community data and use permutation tests to assess statistical significance (Legendre and Anderson 1999, McArdle and Anderson 2001, Anderson 2001a,b). Distance-based MANOVA was based on the same dissimilarity measure used for NMDS ordination: the Bray-Curtis index calculated from line-intercept data standardized by species' maximum. We used software downloaded from the web site of M. J. Anderson (http://www.stat.auckland.ac.nz/~mja). Unfortunately, methods for analyzing the full experimental design with multispecies response data have not yet been developed. As a compromise, we therefore applied distance-based MANOVA to the community data from the three-way factorial design at discrete sampling times: the initial year of data for each site (usually 2000, but 2001 for three sites) and the final year (2004). Fire frequency treatment (F2, F4) was included in the model for the initial year to check for unintentional differences in community composition between fire frequency groups, due to random assignment of sites to treatments. The design matrices coding the experimental design were prepared using the program XMATRIX (Anderson 2003). Pseudo-F statistics and permutation tests were then performed using the program DISTLM (Anderson 2004a).

Indicator Species Analysis or ISA (Dufrêne and Legendre 1997) was used to test for species that distinguish among groups of SUs. ISA is based on the concepts of fidelity (the degree to which a species is confined to a particular group) and constancy (the proportion of SUs in a group in which the species occurs). Fidelity (F) and constancy (C) are combined into a single Indicator Value (IV) as follows:

$$\boldsymbol{IV_{kj} = 100F_{kj}C_{kj}}$$

In order to attain a high *IV* a species must be both faithful and constant. The statistical significance of $\boldsymbol{IV}_{\mathbf{max}}$, the highest *IV* attained by a species over all g groups, is tested by a random permutation of group membership among SUs. Indicator Species Analysis was performed using PCORD version 4 (McCune and Mefford 1999). It was applied in parallel with the ANOSIM and distance-based MANOVA analyses, whenever a significant difference among levels of a factor or a significant interaction was detected.

We examined a number of vegetation measures in addition to ground layer community response. Logistic regression was used to compare survivorship of naturally-regenerated woody seedlings and sprouts from 2001 to 2002 among the forest types and between 2-yr and 4-yr fire treatments, heavier and lighter military use sites, and sandy and clayey soils. We used a general linear model (proc Genmod, SAS v. 9.1) to test differences in longleaf regeneration among forest types, military use categories, soil textures, and fire intervals in 2004.

Focused studies

- Short-term fire effects: Two-factor analysis of variance (ANOVA) was used to compare 'fire effect' (post-fire vs. pre-fire measures) among stands. Analyses of seasonal responses also included a comparison of results on the sandy vs. clayey soils. No fire effect x stand interactions were significant at the alpha = 0.05 level for any analysis.
- Soil respiration: For the one accidentally burned stand, we present post-fire data only from the unburned portions; these partial data were not included in the statistical comparisons of soil CO_2 efflux treatments. Analysis of variance (proc GLM, SAS Institute 2000) was used to test for differences in microbial biomass carbon and fine root production between treatments and 2003 comparisons of total soil CO_2 flux and surface root generated CO_2 efflux. Multiple regression, with forward and backward selection, was used to determine the relationships between soil CO_2 efflux and each of the following: volumetric soil water content, depth of soil A layer, organic layer mass, soil percent clay, and soil temperature. Multicollinearity was tested using variance inflation measures (SAS Institute 2000, Graham 2003).
    - Permanent wilting points W_p, based on soil texture data collected at each soil CO_2 efflux sampling point, were calculated to partition the data into measurements above and below a favorable soil moisture threshold (Saxton et al. 1986). The

thresholds were determined for each site, and represent an approximate matric potential of –1500 Kpa, intended to represent the lower limit of plant available water. Individual multiple regressions were performed for: 1) growing season and non-growing season samples from 2) clayey and sandy stands during 3) periods above and below W_p, to examine the influence of explanatory variables on different soil textures during periods of differing water availability.

- Legume and ground cover: Differences in mean aboveground biomass between fire treatments (2-year, 4-year) and soil texture (sandy, clayey) were determined using a mixed model analysis of variance (ANOVA) with year, site, fire, and texture as fixed effects and subplot as a random effect (PROC MIXED; SAS, 2000). Statistically significant differences between plant groups were determined using the Bonferroni test of multiple pairwise comparisons. Differences in belowground biomass, plant C and N tissue concentrations, and legume N_2-fixation rates and above- and belowground biomass were determined using ANOVA. Statistically significant differences were accepted at $\alpha \leq 0.05$.
- Avian species as indicators of disturbance: Results focus on seven resident or neotropical migratory species associated with open pine-grasslands or early successional habitats and on seven resident or neotropical migratory forest and habitat generalist species common to Fort Benning. We compared abundance among land use categories for individual species and for combined species abundance of early successional and pine-grassland species (brown-headed cowbird abundance was not used in this analysis because of its very low occurrence in our study) and combined species abundance of forest species and habitat generalists. Analysis of variance was used to test differences among the four land use categories for species abundance and habitat variables. Tukey's standardized range test was used to compare means among land use categories. A one-way ANOVA was used to test differences in disturbance (m of line "disturbed" per 600 m transect sampled) between heavy and light use categories.

Results and Accomplishments

Initial site conditions: soil properties

Results of the summer, 2000, baseline surveys of soil texture, disturbance features, and vegetation among the 32 upland forest sites were summarized in 'Soil texture, land-use intensity, and vegetation of Fort Benning upland forest sites' by John Dilustro, Beverly Collins, Lisa Duncan, and Rebecca Sharitz, published in the Journal of the Torrey Botanical Society 129(4):280-297.

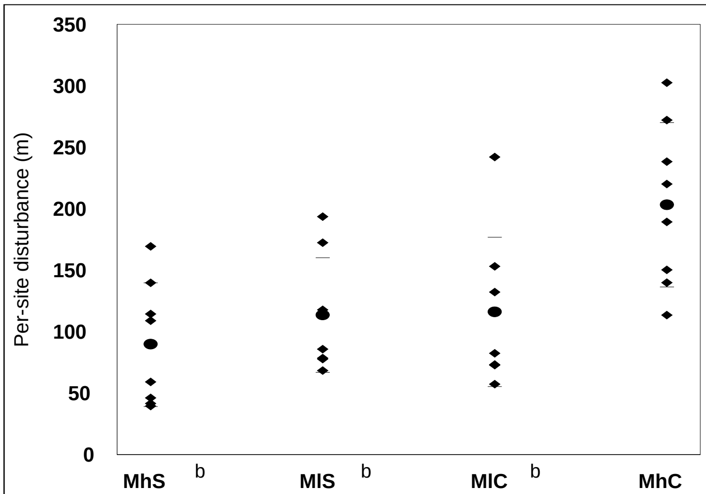


Figure 3. Mean (circle) and standard deviation (lines) of disturbance features in each military training/soil texture category. Also shown are the means for each site within the category (diamonds).

The survey of disturbance features revealed that land-use (forestry or military training-generated) or natural disturbance features occupied from 7% to 50% of sample transect length; half of the sites were at least 30% disturbed. The amount of disturbance differed among the land use/ soil texture categories (ANOVA df=3; ms=19822; F=6.19; p=0.002; Fig. 3). Clayey sites in heavy military use areas (MhC sites) had greater length of sampling transects in disturbance features (Fig. 3). Features included those due to natural disturbance (e.g., treefalls), forestry practices (e.g., skidders), and military use (e.g., tank tracks), or some combination of these (e.g., mounds that could have been left by treefalls, harvesting, or military use) (Fig. 4).

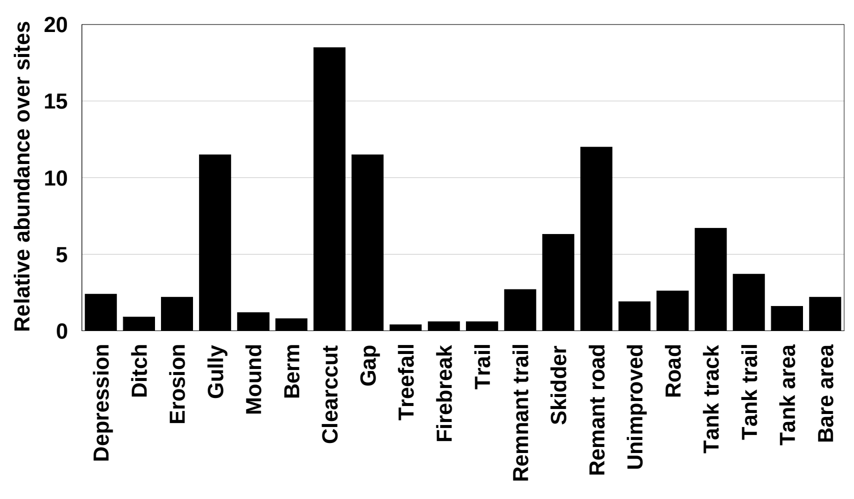


Figure 4. Relative abundance of disturbance features.

Over all sites, gullies were the most frequently encountered disturbance feature, and clearcuts were the most abundant (Fig. 4). However, road-like features, including active and remnant trails, roads, and vehicle tracks or trails, were, collectively, the most frequent and abundant disturbance (Fig. 4).

Before Fort Benning was established, farming practices typical of the region depleted topsoil and soil fertility (Jones and Davo 1997). The historical land use and current forest management, together with military use, are manifest in patterns of soil properties, including texture, carbon, and nitrogen, across the 32 stands. Average soil clay content ranged from 2 % for a sandy site to 48 % for a clayey site; sand content ranged from 32 % for a clayey site to 91 % for a sandy site (Fig. 5). Clayey sites generally had greater variation in percent clay and sand among and within sites. In addition, there was significant interaction between military land-use and soil texture (ANOVA; df=1; ms=3332; F=23.2; p<0.0001); average clay content of sites in heavier training compartments was less than that in sites with lighter training (Fig. 5).

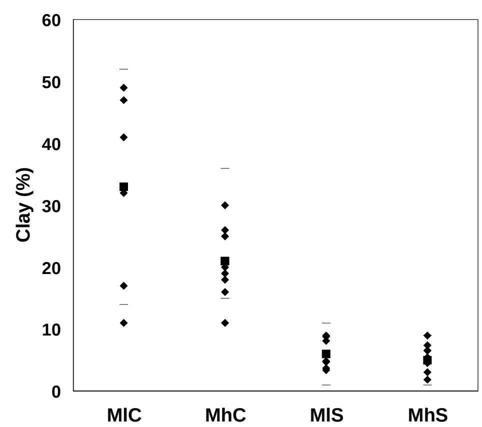


Figure 5. Clay content (%) of sites with sandy (S) or clayey (C) soils and heavier (Mh) or lighter (Ml) training. Shown are categories means (circles) and standard deviations (lines) as well as means (diamonds) for each site in a category.

In 2001, average organic layer mass was greatest in sites with clayey soil ($F_{1,28} = 4.69$, $p < 0.039$); this reflects the higher tree density on these sites (Dilustro et al. 2002). Nitrogen content of the organic layer did not differ significantly among soil texture or land use categories. The organic layer nitrogen pool was greater, though not significantly, in light use sites ($F_{1,28} = 3.06$, $p < 0.091$). Organic layer carbon concentration (%C; $F_{1,28} = 4.47$, $p < 0.044$) was greater in clayey sites and the organic layer carbon pool (g C/m^2; $F_{1,28} = 5.83$, $p < 0.023$) was greater in light use sites. The organic layer C:N ratio ranged from 51 and 53 in clayey sites to 57 in sandy sites (Table 1). A relatively high C:N is characteristic of conifer litter and/or sites where low soil fertility limits the quality of litter produced. It indicates a slowly decomposing organic matter pool and decreased nitrogen availability (Paul & Clark 1996).

Variable	Clayey soil		Sandy soil	
	Lighter use	Heavier use	Lighter use	Heavier use
Mass (g/m^2)	1158 (100)	925 (74)	917 (96)	803 (100)
C concentration (%)	39 (0.99)	34 (1.2)	41 (1.0)	39 (1)
Carbon stock (g C m^{-2})	441 (35)	303 (25)	344 (28)	304 (32)
N concentration	0.70 (0.03)	0.65 (0.02)	0.73 (0.02)	0.68 (0.02)
Nitrogen pool (g N m^{-2})	8.27 (0.81)	5.71 (0.42)	6.33(0.58)	5.79 (0.93)
C: N ratio	51 (2.6)	53 (1.9)	57 (2.1)	57 (2.5)

Table 1. Mean and (standard error) of soil organic layer (OL) mass, carbon concentration, carbon stock, nitrogen stock, nitrogen concentration and C:N ratio for 32 forest stands grouped into four use/texture combinations (N=8 stands per category). Lower case subscripts indicate significant differences among treatment combinations (P<0.05).

Soil bulk density differed among sites with respect to land use and soil texture (Table 2). Bulk density was greater in sandy compared to clayey soil ($F_{1,28} = 4.70$, $p < 0.039$) and with heavier compared to lighter military use intensity ($F_{1,28} = 4.56$, $p < 0.042$). Mineral soil nitrogen concentration, however, had a significant soil * land use interaction ($F_{1,28} = 8.27$, $p < 0.008$); the increase in soil nitrogen was greater on the light use sites on clayey soils (texture - $F_{1,28} = 23.02$, $p < 0.001$; land use intensity- $F_{1,28} = 11.81$, $p < 0.002$). Mineral soil nitrogen pool reflected the nitrogen concentration and had a significant soil * land use interaction ($F_{1,28} = 9.11$, $p < 0.006$); the increase in soil nitrogen pool was greater on the light use sites on clayey soils (texture - $F_{1,28} = 18.74$, $p < 0.001$; land use intensity- $F_{1,28} = 5.18$, $p < 0.031$). Soil % carbon was influenced by texture, with greater concentrations in clayey soils ($F_{1,28} = 10.90$, $p < 0.003$). Soil % carbon also was influenced by land use, with lighter land use ($F_{1,28} = 8.39$, $p < 0.007$) exhibiting greater carbon concentrations. Mineral soil carbon pool reflected the carbon concentration and had a significantly greater soil carbon pool on the light use sites and clayey soils (texture - $F_{1,28} = 7.66$, $p < 0.010$; land use intensity- $F_{1,28} = 6.42$, $p < 0.017$). Mineral soil C:N ratio did not differ among treatment combinations.

Variable	Clayey soil		Sandy soil	
	Light use	Heavy use	Light use	Heavy use
Bulk density (g cm^{-3})	1.17 (0.03)	1.25 (0.03)	1.27 (0.04)	1.40 (0.03)
C concentration (%)	2.03 (0.17)	1.32 (0.19)	1.16(0.10)	0.92 (0.10)
C stock (g C m^{-2})	3539.27 (301.00)	2428.13 (348.01)	2139.63 (171.15)	1899.11 (205.40)
N concentration (%)	0.081 (0.007)	0.042 (0.003)	0.036(0.003)	0.031 (0.002)
N stock (g N m^{-2})	141.28 (12.96)	77.34 (4.75)	65.35(5.40)	64.91 (3.24)
C:N ratio	26.37 (1.29)	29.22 (1.91)	34.42 (1.70)	28.88 (2.33)

Table 2. Mean and (standard error) of mineral soil bulk density, carbon concentration, carbon stock, nitrogen concentration, nitrogen stock and C:N ratio for the 32 forest stands grouped into soil texture and land use categories (N=8 or 16 stands per category). Lower case subscripts indicate significant differences among treatment combinations (P<0.05).

In 2001, extractible NH_4-N was significantly higher in sites with clayey soil ($F_{1,28} = 6.42$, $p < 0.017$) and lighter military use ($F_{1,28} = 10.95$, $p < 0.003$) (Fig. 6a). Initial NO_3-N was greater in sandy sites ($F_{1,28} = 4.82$, $p < 0.037$). Nitrate production began immediately during the first 42-day incubation period in all sites (Fig. 6b). This suggests there was no delay in nitrification and the process was active in all sites. Both NO_3-N and NH_4-N cumulative production increased substantially throughout the second incubation period (Fig. 6c).

In the first 42-day incubation period, soil from sandy sites with heavier military use had significantly greater ($F_{1,28} = 8.93$, $p < 0.006$) NO_3-N production (Fig. 6b). NH_4-N production was significantly greater on clayey sites ($F_{1,28} = 4.83$, $p < 0.036$). Sandy sites and heavier military use stands continued to have significantly greater (texture - $F_{1,28} = 6.77$, $p < 0.015$; land use intensity- $F_{1,28} = 4.22$, $p < 0.049$) NH_4-N production through the end of the second incubation period (Fig. 6c). NO_3-N production was highest ($F_{1,28} = 11.20$, $p < 0.002$) for clayey sites and lowest ($F_{1,28} = 11.39$, $p < 0.002$) for lighter use sites (Fig. 6c). Overall, net nitrification significantly differed among land use/soil texture factors (texture - $F_{1,28} = 10.92$, $p < 0.003$; land use intensity- $F_{1,28} = 11.29$, $p < 0.002$). Net nitrification was greater for sandy sites and those with heavier military use.

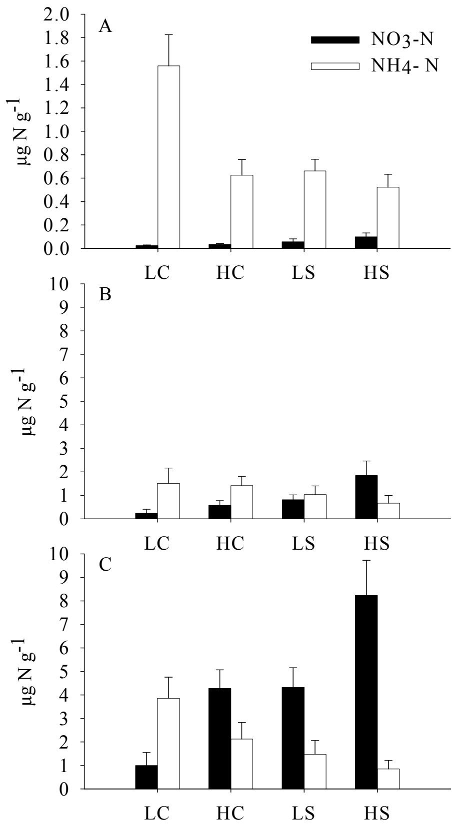


Figure 6. Mean (+ std. error) extractable soil NO_3-N and NH_4-N. A) Initial extraction; B) After aerobic 42-day incubation; C) Cumulative production after aerobic 84-day incubation. LC = lighter use/clayey soil, LS=light use/sandy soil, HC=heavy use/ clayey soil), HS=heavy use/sandy soil.

Overall, differences in soil properties among the 32 upland forest stands were related to soil texture and military land use intensity. The collective results suggest organic layers in sandy compared to clayey sites could immobilize nitrogen through relatively slow rates of decomposition and nitrogen release to the mineral soil. In the mineral soil, field and laboratory results suggest that mineralization processes enhance nitrogen availability in sandy sites, especially in land compartments with heavier military training. In the laboratory incubations, mineral soils from the sandy sites in heavier military use compartments produced significantly more NO_3-N, which suggests mineralization processes differ in these sites (soils from other sites produced less NO_3-N and more NH_4-N). Further, there is greater potential for nitrogen to be available for vegetation (uptake) with disturbance. Results from the laboratory Nmin studies and plant-root-simulator probes also indicate greater nitrogen production and availability in sandy compared to clayey sites.

In contrast to the sandy sites, greater organic layer mass and initial extractable mineral soil nitrogen in clayey sites, particularly in sites with lighter military use, reflect the effects of finer soil texture and the lower impact of military training on the loss of the organic layer.

Greater organic layer mass and nitrogen content favor faster decomposition (Prescott et al. 2000) and release of nitrogen for mineralization in these sites, but the lower nitrogen availability we observed in the field (on the heavier use sites) suggests mineralized nitrogen can be bound by fine soil particles. Additional factors such as soil type and litter composition may influence N processing on these sites. Despite the greater organic layer mass and nitrogen content on the clayey sites with lighter military use, these sites had the lowest net nitrification and percent relative nitrification rates. The PRS probe tests showed no significant effect of texture on NH_4 but significantly greater NO_3. This is consistent with the greater extractable NO_3 pool measured on these sites.

Initial site conditions: vegetation

Non-metric multi-dimensional scaling (NMDS) was used to visualize initial (2000, 2001) vegetation patterns among the sites. There was a strong effect of military training on canopy and ground layer composition (Fig. 7). In general, both sandy and clayey sites in the lighter training category (Ml) grouped in the upper left quadrant of the canopy tree plot and to the left of the y-axis in the ground layer vegetation plot (Fig. 7). One site in the Ml category, site A15, appears compositionally more related to sites with heavier military training (Fig. 7). This site tends to burn more frequently than the 3-year cycle of the other sites, and the canopy is > 90% longleaf pine.

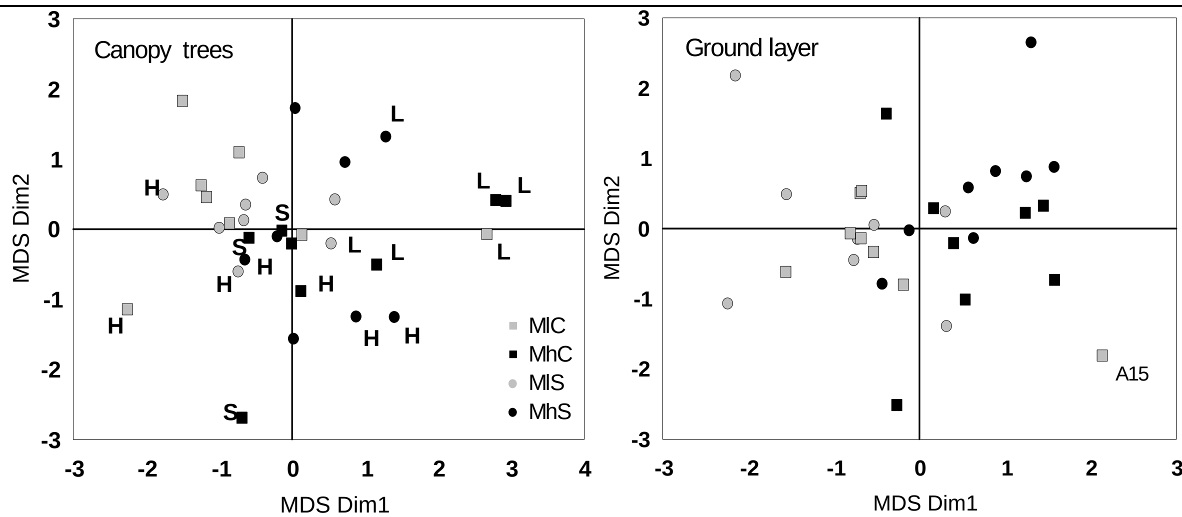


Figure 7. NMDS ordination of canopy tree and ground layer composition in sandy (S) and clayey (C) sites with heavier (Mh) or lighter (Ml) military training. Letters denote canopy composition: L = sites with significant (> 50 %) longleaf pine; S = sites with > 50 % shortleaf pine; H = mixed pine-hardwood sites with > 50 % hardwoods; sites without a letter = > 50 % loblolly pine canopy.

The proportion of pine, particularly longleaf pine, also is reflected in the canopy tree ordination (Fig. 7). We distinguished four forest types, based on the dominant canopy trees: longleaf pine stands (L) are > 85 % pine and > 50 % longleaf; shortleaf stands (S) are 78 – 94 %

pine and > 50 % shortleaf; mixed pine hardwood stands (H) range from 12 – 50 % pine, mostly loblolly; and loblolly stands (no letter) range from 51-99% pine, with > 50 % loblolly.

Ground layer vegetation also reflected the canopy dominant. Although the ordination suggests less pronounced differences among forest types in ground layer compared to canopy vegetation (Fig. 7), pine-hardwood and longleaf stands had different ground layer composition in 2000 [Table 3; different letters indicate significant difference ($P < 0.05$)]. *Andropogon* sp., primarily broomsedge, *A. virginicus*, *Pityopsis*, and sweetgum (*Liquidambar*) seedlings were abundant in multiple canopy types. Pine-hardwood forests had abundant *Vitis* sp, while bracken fern (*Pteridium aquilinum*) was abundant in longleaf stands (Table 3). The abundance of legumes and grasses was higher in the longleaf stands than in the other forest types (Table 3).

	Pine Hardwood	**Longleaf**	**Shortleaf**	**Loblolly**
2000	b	a	ab	ab
Dominants	*Vitis* sp.; *Liquidambar styraciflua*; *Andropogon* sp.	*Andropogon* sp.; *Pteridium aquilinum*; *Pityopsis graminifolia*	*Andropogon* sp.; *Smilax* sp.; *Pityopsis graminifolia*	*Liquidambar styraciflua*; *Andropogon* sp.; *Pityopsis graminifolia*
legumes, grasses	32 ± 16	59 ± 32	37 ± 8	32 ± 13

Table 3. Initial (yr 2000) ground layer composition differences among forest canopy types

Table 4 shows the distribution of the 32 upland forest sites among forest types and the land use/soil texture categories. Loblolly stands are over-represented in some land use/soil texture combinations. In contrast, there are no longleaf stands in the 4-yr fire treatment; this likely occurred because these stands are in landscape compartments that are managed using frequent prescribed fire.

	F2MlS	F2MhS	F2MlC	F2MhC	F4MlS	F4MhS	F4MlC	F4MhC	Total
Pine-Hardwood	1	1	1		1	2	1	1	8
Longleaf	2	1	2	2					7
Loblolly	1	2	1	1	3	1	3	1	13
Shortleaf				1		1		2	4
Total	4	4	4	4	4	4	4	4	32

Table 4. Distribution of SREL field sites among forest types and land use categories. F2,4 = 2-yr or 4-yr prescribed fire treatment; Ml,h = lighter or heavier military use; S,C = sandy or clayey soil

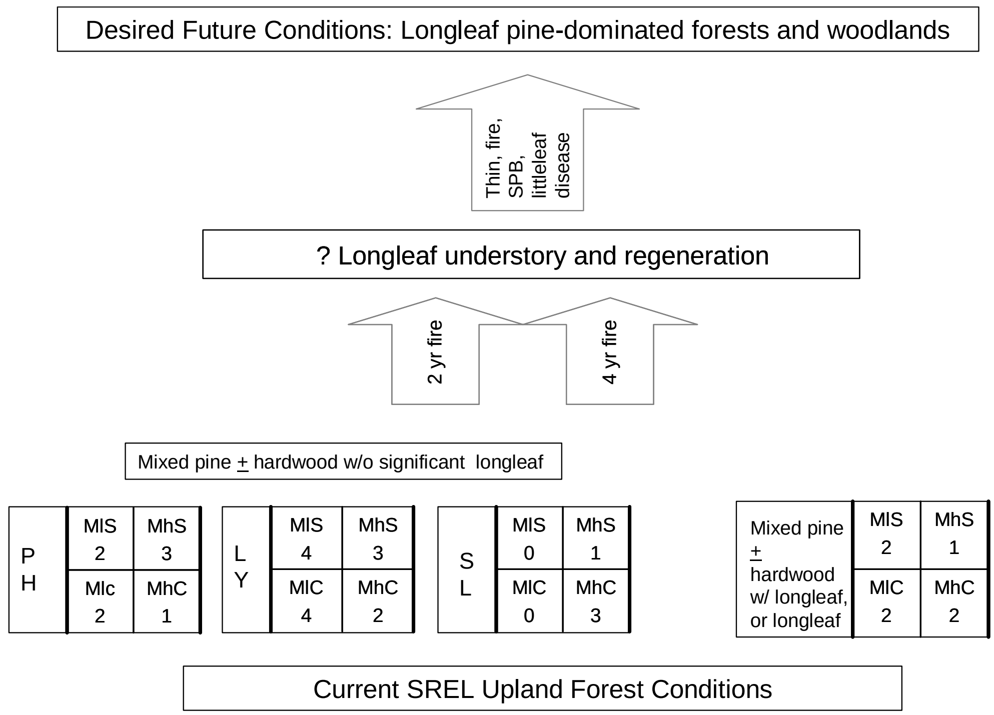


Figure 8. SREL field sites within the Fort Benning ecological restoration model.

Figure 8 shows SREL sites, land conditions, and forest management treatments (prescribed fire interval) within Fort Benning's ecological restoration model. The distribution of sites among soil texture (S,C) and military training (Ml,Mh) categories is shown for mixed-pine hardwoods (PH), loblolly (LY), and shortleaf (SL) stands without significant longleaf, as well as longleaf-dominated stands. Within this model, SREL research tested whether a shorter (2-yr) or longer (4-yr) prescribed fire a) increases pine regeneration and accelerates the transition to longleaf forest, b) causes no change in regeneration and maintains the current forest, or c) initiates a transition to a different domain (i.e, regeneration and nitrogen cycling do not reflect either current composition or longleaf pine ecosystem). We also tested if soil type or military training influences the prescribed fire effects. **Under the assumption that a short (2-yr) fire interval is the external force that sustains longleaf ecosystem, sandy or clay longleaf-dominated sites with lower or higher military use and in the 2-yr fire treatment provided 'control' or threshold values for transition to the longleaf ecosystem domain.**

One 4-yr fire site (4HS) accidentally burned in late 2002; a second site (4LS) was prescribe-burned to balance over the military use categories. Table 5 shows the distribution of remaining 30 sites over vegetation and land use categories:

	F2MlS	F2MhS	F2MlC	F2MhC	F4MlS	F4MhS	F4MlC	F4MhC	Total
Pine-Hardwood	1	1	1			1	1	1	6
Longleaf	2	1	2	2					7

Loblolly	1	2	1	1	3	1	3	1	13
Shortleaf				1		1		2	4
Total	4	4	4	4	3	3	4	4	30

Table 5. Distribution of SREL field sites among forest types and land use categories following loss of two sites. F2,4 = 2-yr or 4-yr prescribed fire treatment; Ml,h = lighter or heavier military use; S,C = sandy or clayey soil

Results after four years: ground layer vegetation

Examination of the scree-plot (minimum stress vs number of dimensions) for the NMDS ordination of the entire data set and vector fitting results for explanatory variables indicated that three dimensions offered the best representation of the pattern of community variation among sites. To facilitate visual interpretation, the ordination axes were rigidly rotated. Full results of vector fitting in the rotated 3-dimensional NMDS ordination are shown in Table 6. All four of the experimental design variables, Military Use, Soil Type, Fire Frequency and Year were significantly correlated with the NMDS ordination in three dimensions.

Variable	*r*	*p*	Direction Cosines		
			Axis 1	Axis 2	Axis 3
Military Use	0.6005	<0.0001	1.0000	0.0000	0.0000
Soil Type	0.5963	<0.0001	-0.2543	0.9671	0.0000
Burn Frequency	0.5186	<0.0001	-0.6845	-0.6713	-0.2843
Year	0.2805	0.0066	-0.1502	0.0070	0.9886
Richness	0.7170	<0.0001	0.0633	0.3371	0.9393
Total Abundance	0.7195	<0.0001	0.0102	0.3333	0.9428
Shannon Diversity	0.3160	0.0015	-0.2034	-0.1313	0.9703
Shannon Evenness	0.2796	0.0073	-0.5076	-0.8615	0.0098

Table 6. Full results of vector fitting in 3-dimensional NMDS ordination. For each variable, the correlation (r) between values of that variable and SU scores on its fitted vector is shown, together with the probability (p) from the permutation test for statistical significance of the correlation. The direction cosines define the direction of the vector with respect to the three axes of the ordination, which has been rotated to align the plane of axes 1 and 2 with the fitted vectors for Military Use and Soil Type.

Figures 9-11 show the rotated NMDS ordination of the ground layer vegetation (only 2 axes shown); each is annotated to contrast levels of military use, fire frequency, or soil texture. Points representing the same site sampled in each year are connected by a time trajectory, the arrow head terminating at the point for 2004. Fitted vectors for Military Use, Soil Type, Burn Frequency, Year and Richness are overlaid. The length of the fitted vectors in the full three-dimensional ordination space is proportional to their correlation, but their apparent length on a bivariate plot depends on the degree to which the vector diverges into the other dimension.

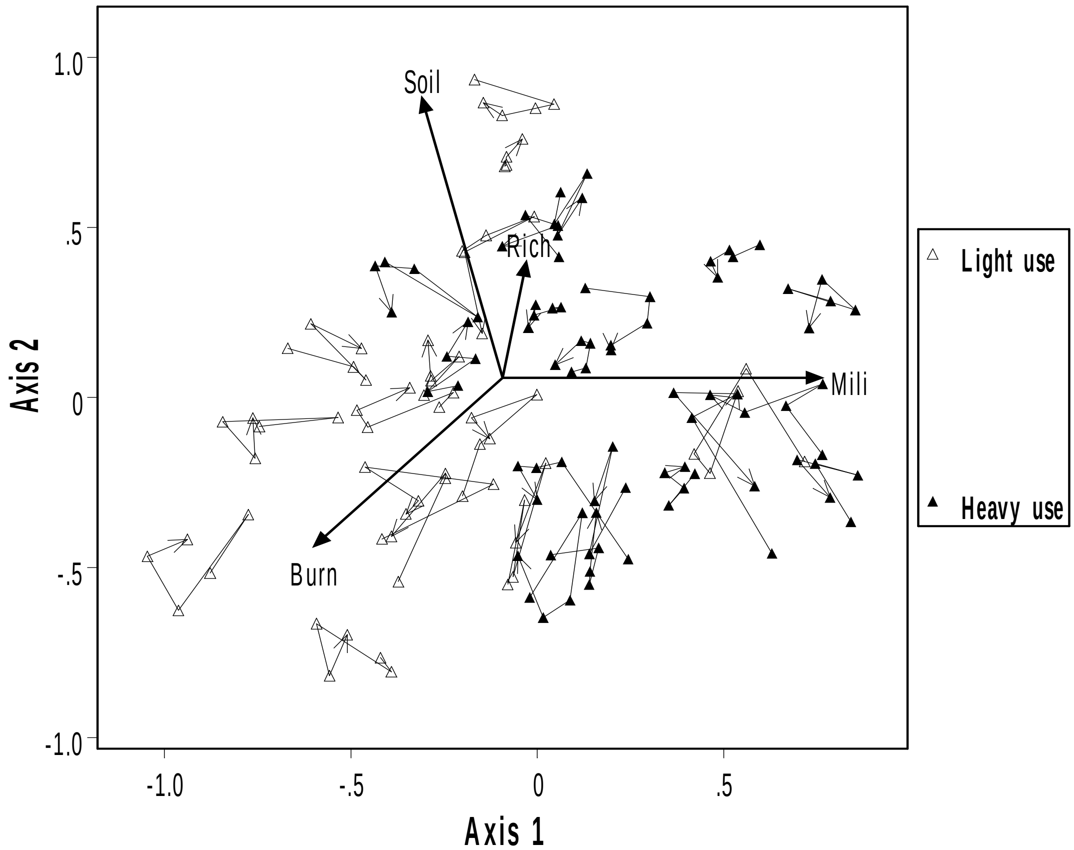


Figure 9. NMDS ordination of ground layer vegetation, with sites annotated to show Military Use. Points for each site are joined in chronological order, with an arrow head pointing to the final year's point. Fitted vectors of maximum correlation are overlaid for Military Use (Mili), Soil Type (Soil), Burn Frequency (Burn) and Site Richness (Rich).

As shown in Fig. 9, the ordination of ground layer vegetation suggests a difference in community composition between sites with lighter and heavier Military Use, with lightly disturbed sites (open symbols) to the left on rotated axis 1 and heavily disturbed sites to the right. This difference was confirmed by an overall ANOSIM test for Military Use (R=0.1986, p<0.0001). In addition, separate ANOSIM tests using the data from each sampling year show that there was a significant difference in community composition between Military Use levels in every year (Table 7).

Factor	**Initial** (*n* = 31)		**2000** (*n* = 28)		**2001** (*n* = 30)		**2002** (*n* = 31)		**2003** (*n* = 31)		**2004** (*n* = 31)	
	R	***p***	***R***	***p***	***R***	***p***	***R***	***p***	***R***	***p***	***R***	***p***
Soil Texture	**0.2235**	0.0003	**0.1769**	0.0027	**0.2232**	0.0004	**0.2139**	0.0010	**0.1594**	0.0041	**0.2297**	0.0001

Military Use	**0.1473**	0.0059	**0.1821**	0.0021	**0.1434**	0.0086	**0.1637**	0.0052	**0.1523**	0.0044	**0.1489**	0.0033
Fire Freq	0.0440	0.1494	0.0369	0.2094	0.0479	0.1359	**0.2437**	0.0006	**0.0785**	0.0418	**0.1126**	0.0126

Table 7. ANOSIM tests of differences in community composition between levels of each experimental factor. Separate tests were conducted in each sampling year (2000 through 2004) and also using the first available year of data for each site (Initial). The total number of sites in each test (n) is indicated. The ANOSIM statistic, R, is shown along with probability (p) based on 10,000 random permutations of group membership.

Indicator species analysis, using the combined data from all years, identified 33 species that are indicators of lighter use sites and 43 species that are characteristic of heavier use sites (Table 8). Most of these were relatively less abundant (< 1 %) species. However, abundant indicator species for heavier military use areas included *Andropogon* sp., *Quercus margaretta*, *Gelsemium sempervirens*, *Smilax* sp., *Rhus aromatica*, and *Tephrosia virginiana*. Of these taxa, *Andropogon*, *Q. margaretta*, and *T. virginiana* are common in fall line sandhills communities (Workman and McLeod 1990). In addition, seven legume species were indicators of heavier military use sites. Abundant (≥ 1 %) indicator species of lighter military use sites inlcuded *Liquidamber styraciflua*, *Myrica cerifera*, *Vaccinium stamineum*, *Cyrilla racemiflora*, *Arundinaria gigantea*, and *Quercus nigra*. Of these taxa, *M. cerifera*, *C. racemiflora*, *A. gigantea*, and *Q. nigra* can be common in more mesic or wetter sites (Workman and McLeod 1990). Overall, the indicator analyses suggest sites with heavier military use are characterized by more sandhills-like vegetation while sites with lighter military use have more mesic or broadly distributed species.

Species	**Growth Form**	**Military Use**		***p***
		Lighter	**Heavier**	
Osmunda sp.	Fern	**13**	0	0.0006
Agave virginica	Forb	**9**	0	0.0089
Angelica venenosa	Forb	**11**	0	0.0150
Coreopsis major	Forb	**44**	13	0.0018
Elephantopus tomentosus	Forb	**56**	23	0.0003
Ruellia sp.	Forb	**16**	2	0.0168
Senecio sp.	Forb	**6**	0	0.0407
Aristida sp.	Graminoid	**7**	0	0.0162
Arundinaria gigantea	Graminoid	**41**	0	0.0001
Carex sp.	Graminoid	**64**	28	0.0007
Poaceae sp3.	Graminoid	**13**	0	0.0007
Uniola sessiliflora	Graminoid	**50**	2	0.0001
Pueraria lobata	Legume	**7**	0	0.0187
Stylosanthes biflora	Legume	**42**	16	0.0448
Alnus serrulata	Shrub	**7**	0	0.0170
Aralia spinosa	Shrub	**14**	1	0.0094
Callicarpa americana	Shrub	**35**	5	0.0005
Cyrilla racemiflora	Shrub	**7**	0	0.0170
Myrica cerifera	Shrub	**66**	14	0.0001
Rhus vernix	Shrub	**6**	0	0.0391
Vaccinium elliottii	Shrub	**38**	15	0.0274
Vaccinium myrsinites	Shrub	**33**	0	0.0001

Vaccinium stamineum	Shrub	**65**	24	0.0002
Acer rubrum	Tree	**42**	5	0.0008
Cercis canadensis	Tree	**16**	0	0.0002
Fraxinus americana	Tree	**13**	0	0.0008
Liquidambar styraciflua	Tree	**63**	24	0.0002
Quercus alba	Tree	**20**	6	0.0478
Quercus nigra	Tree	**55**	26	0.0154
Campsis radicans	Vine	**19**	2	0.0049
Mitchella repens	Vine	**13**	0	0.0008
Parthenocissus quinquefolia	Vine	**29**	4	0.0028
Passiflora incarnata	Vine	**9**	0	0.0079
Agrimonia sp.	Forb	0	**11**	0.0069
Ambrosia artemisiifolia	Forb	0	**19**	0.0062
Aster paternus	Forb	6	**28**	0.0413
Asteraceae sp1.	Forb	30	**52**	0.0394
Chrysopsis gossypina	Forb	0	**10**	0.0276
Chrysopsis mariana	Forb	11	**30**	0.0443
Cnidoscolus stimulosus	Forb	3	**51**	0.0002
Commelina virginica	Forb	2	**19**	0.0121
Diodia teres	Forb	0	**46**	0.0001
Eryngium yuccifolium	Forb	0	**14**	0.0010
Eupatorium hyssopifolium	Forb	15	**40**	0.0146
Euphorbia corollata	Forb	14	**35**	0.0337
Helianthemum rosmarinifolium	Forb	0	**10**	0.0164
Heterothica graminifolia	Forb	23	**76**	0.0001
Hieracium gronovii	Forb	7	**29**	0.0316
Hypericum gentianoides	Forb	3	**34**	0.0010
Liatris sp.	Forb	10	**37**	0.0058
Oxalis sp.	Forb	2	**21**	0.0129
Polypremum procumbens	Forb	0	**31**	0.0001
Rudbeckia sp.	Forb	0	**17**	0.0006
Silphium dentatum	Forb	0	**11**	0.0068
Stipulicida setacea	Forb	0	**16**	0.0017
Tragia urens	Forb	4	**40**	0.0002
Andropogon sp.	Graminoid	35	**63**	0.0010
Tripascum dactyloides	Graminoid	0	**11**	0.0497
Centrosema virginianum	Legume	9	**48**	0.0002
Dalea purpurea	Legume	0	**7**	0.0310
Rhynchosia reniformis	Legume	6	**35**	0.0129
Rhynchosia tomentosa	Legume	1	**24**	0.0014
Schrankia microphylla	Legume	2	**31**	0.0012
Tephrosia virgininana	Legume	1	**45**	0.0001
Vicia sp.	Legume	3	**18**	0.0435
Rhus aromatica	Shrub	2	**35**	0.0002
Aesculus pavia	Tree	0	**10**	0.0198
Celtis sp.	Tree	1	**30**	0.0002
Crataegus sp.	Tree	13	**62**	0.0001
Ilex opaca	Tree	0	**20**	0.0005
Quercus laevis	Tree	2	**15**	0.0399
Quercus margaretta	Tree	7	**36**	0.0058
Gelsemium sempervirens	Vine	26	**52**	0.0269
Ipomoea sp.	Vine	13	**51**	0.0002

Smilax sp.	Vine	36	**63**	0.0076
Stylisma patens	Vine	3	**32**	0.0049

Table 8. Results of Indicator Species Analysis between levels of Military Use, using combined data from all sampling years. The tabulated values are indicator scores that combine fidelity (the degree to which a species is confined to one level or the other) and constancy (the proportion of sampling units within a level in which the species occurs). The probability (p) is derived as the proportion of times that maximum indicator score obtained under random assignment of sampling units among levels was at least as large as the actual value. Only species that are significant indicators at the 0.05 level are included in the table.

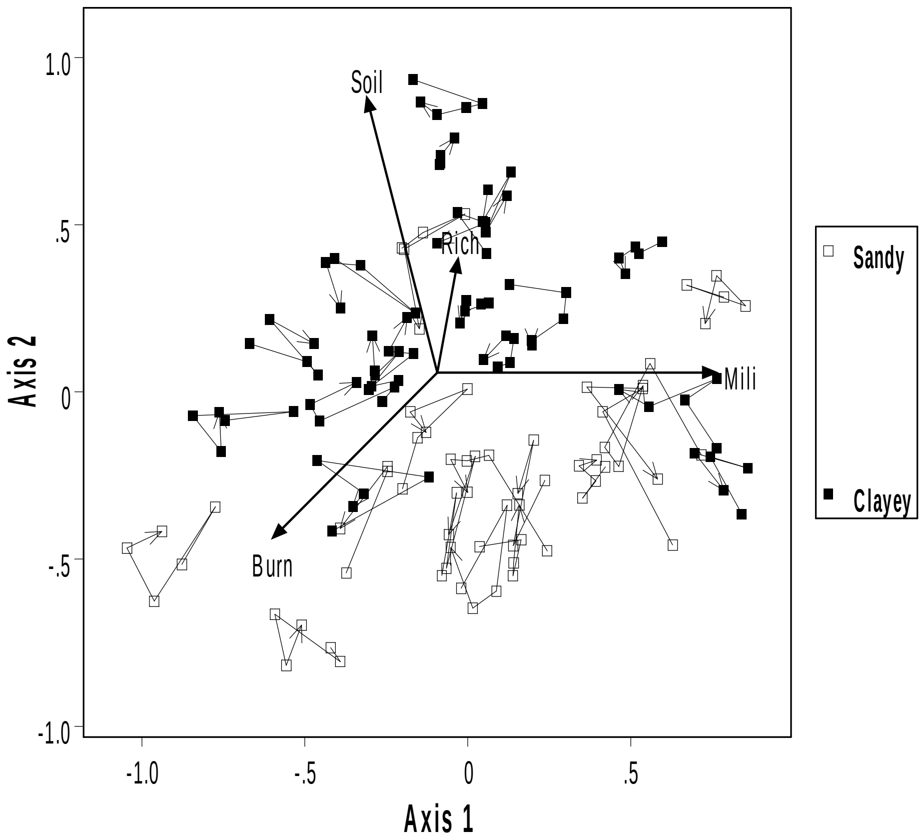


Figure 10. NMDS ordination of ground layer vegetation, with sites annotated to show Soil Texture. Points for each site are joined in chronological order, with an arrow head pointing to the final year's point. Fitted vectors of maximum correlation are overlaid for Military Use (Mili), Soil Type (Soil), Fire Frequency (Burn) and Site Richness (Rich).

A second dimension of the ground layer ordination, approximately in the direction of rotated axis 2 (Fig, 10), separates sites with sandy and clayey soils. An overall ANOSIM test confirms a difference in community composition between soil textures (R=0.2164 , p<0.0001).

As with Military Use, separate ANOSIM tests using the data from each sampling year show that there was a significant difference in community composition between Soil Texture levels in every year (Table 9). Indicator species analysis, using the combined data from all years, identified 41 species that are indicators of sites with sandy soils and 49 species that are characteristic of sites with clayey soils (Table 9). As with military use, most indicator species for soil texture are less common species (< 1 % relative abundance). Abundant indicator taxa of clayey sites include *Andropogon* sp., *Panicum* sp., and one *Aster* sp. (Asteraceae sp1). Abundant indicator taxa of sandy sites include tree seedlings (*Liquidambar styraciflua*, *Quercus laurifolia*, *Q. margaretta*, and *Q. nigra*), vines (*Gelsemium sempervirens* and *Vitis* sp.), and shrubs (*Cyrilla racemiflora*, *Ilex glabra*, and *Vaccinium stamineum*). There were no graminoid indicators of sandy sites and, in general, fewer legume and forb indicators in sandy, compared to clayey, sites.

Species	**Growth Form**	**Soil Texture**		***p***
		Sandy	**Clayey**	
Osmunda sp.	Fern	**12**	0	0.0052
Aureolaria sp.	Forb	**19**	0	0.0005
Carduus sp.	Forb	**8**	0	0.0359
Cnidoscolus stimulosus	Forb	**57**	3	0.0001
Eriogonum tomentosum	Forb	**10**	0	0.0026
Euphorbia corollata	Forb	**35**	15	0.0363
Iris cristata	Forb	**7**	0	0.0154
Paronychia sp.	Forb	**10**	0	0.0030
Solidago nemoralis	Forb	**6**	0	0.0380
Tragia urens	Forb	**35**	7	0.0009
Clitoria mariana	Legume	**30**	5	0.0115
Pueraria lobata	Legume	**7**	0	0.0187
Rhynchosia reniformis	Legume	**42**	5	0.0001
Alnus serrulata	Shrub	**7**	0	0.0183
Amelanchier sp.	Shrub	**6**	0	0.0382
Aralia spinosa	Shrub	**22**	0	0.0001
Bumelia sp.	Shrub	**10**	0	0.0040
Cyrilla racemiflora	Shrub	**7**	0	0.0183
Ilex glabra	Shrub	**27**	5	0.0076
Ilex verticillata	Shrub	**9**	0	0.0069
Rhus vernix	Shrub	**6**	0	0.0392
Symplocos tinctoria	Shrub	**6**	0	0.0360
Vaccinium stamineum	Shrub	**67**	24	0.0001
Yucca filamentosa	Shrub	**22**	1	0.0009
Asimina parviflora	Tree	**8**	0	0.0365
Carya tomentosa	Tree	**52**	17	0.0030
Celtis sp.	Tree	**23**	4	0.0099
Cornus florida	Tree	**38**	17	0.0306
Ilex opaca	Tree	**26**	0	0.0001
Liquidambar styraciflua	Tree	**57**	30	0.0019
Quercus falcata	Tree	**55**	23	0.0031
Quercus laurifolia	Tree	**53**	3	0.0001
Quercus margaretta	Tree	**56**	2	0.0001

Quercus nigra	Tree	**71**	14	0.0001
Sassafras albidum	Tree	**65**	2	0.0001
Epigaea repens	Vine	**6**	0	0.0418
Gelsemium sempervirens	Vine	**62**	18	0.0004
Mitchella repens	Vine	**12**	0	0.0057
Parthenocissus quinquefolia	Vine	**29**	5	0.0025
Stylisma patens	Vine	**45**	2	0.0001
Vitis sp.	Vine	**55**	36	0.0412
Agrimonia sp.	Forb	0	**11**	0.0081
Aster linariifolius	Forb	0	**21**	0.0012
Aster paternus	Forb	1	**46**	0.0001
Asteraceae sp1.	Forb	12	**75**	0.0001
Asteraceae sp2.	Forb	2	**31**	0.0003
Chrysopsis mariana	Forb	7	**37**	0.0013
Collinsonia sp.	Forb	0	**14**	0.0004
Coreopsis major	Forb	10	**47**	0.0004
Elephantopus tomentosus	Forb	22	**54**	0.0005
Eryngium yuccifolium	Forb	0	**14**	0.0009
Eupatorium aromaticum	Forb	11	**40**	0.0055
Eupatorium capillifolium	Forb	3	**18**	0.0482
Eupatorium rotundifolium	Forb	2	**32**	0.0002
Hexastylis arifolia	Forb	0	**14**	0.0018
Lobelia puberula	Forb	1	**12**	0.0463
Oxalis sp.	Forb	2	**19**	0.0277
Solidago odora	Forb	41	**58**	0.0053
Tragia urticifolia	Forb	0	**20**	0.0003
Vernonia angustifolia	Forb	15	**59**	0.0002
Andropogon sp.	Graminoid	35	**63**	0.0006
Carex sp.	Graminoid	35	**56**	0.0424
Gymnopogon ambiguus	Graminoid	3	**23**	0.0090
Panicum sp.	Graminoid	26	**73**	0.0001
Paspalum sp.	Graminoid	1	**20**	0.0169
Poaceae sp1.	Graminoid	8	**48**	0.0002
Poaceae sp2.	Graminoid	0	**25**	0.0001
Poaceae sp3.	Graminoid	0	**11**	0.0072
Poaceae sp4.	Graminoid	34	**62**	0.0038
Tripascum dactyloides	Graminoid	0	**13**	0.0058
Uniola sessiliflora	Graminoid	3	**39**	0.0001
Cassia sp.	Legume	28	**59**	0.0123
Centrosema virginianum	Legume	11	**46**	0.0011
Lespedeza sp.	Legume	30	**53**	0.0222
Strophostyles umbellata	Legume	4	**32**	0.0022
Stylosanthes biflora	Legume	12	**49**	0.0030
Tephrosia spicata	Legume	6	**49**	0.0001
Vicia sp.	Legume	1	**25**	0.0012
Rubus sp.	Shrub	37	**63**	0.0001
Aesculus pavia	Tree	0	**12**	0.0043
Cercis canadensis	Tree	0	**13**	0.0021
Crataegus sp.	Tree	22	**49**	0.0222
Fraxinus americana	Tree	0	**11**	0.0073

Liriodendron tulipifera	Tree	0	**12**	0.0049
Pinus taeda	Tree	1	**22**	0.0052
Quercus alba	Tree	1	**28**	0.0003
Quercus stellata	Tree	2	**30**	0.0003
Ulmus alata	Tree	4	**24**	0.0243
Campsis radicans	Vine	1	**21**	0.0021
Smilax sp.	Vine	36	**64**	0.0054

Table 9. Results of Indicator Species Analysis between levels of Soil Texture, using combined data from all sampling years. For more explanation, see caption of Table 8.

As shown in Fig. 11, a trend in community composition associated with Fire Frequency falls close to the plane defined by the fitted vectors for Military Use and Soil Texture. The fitted

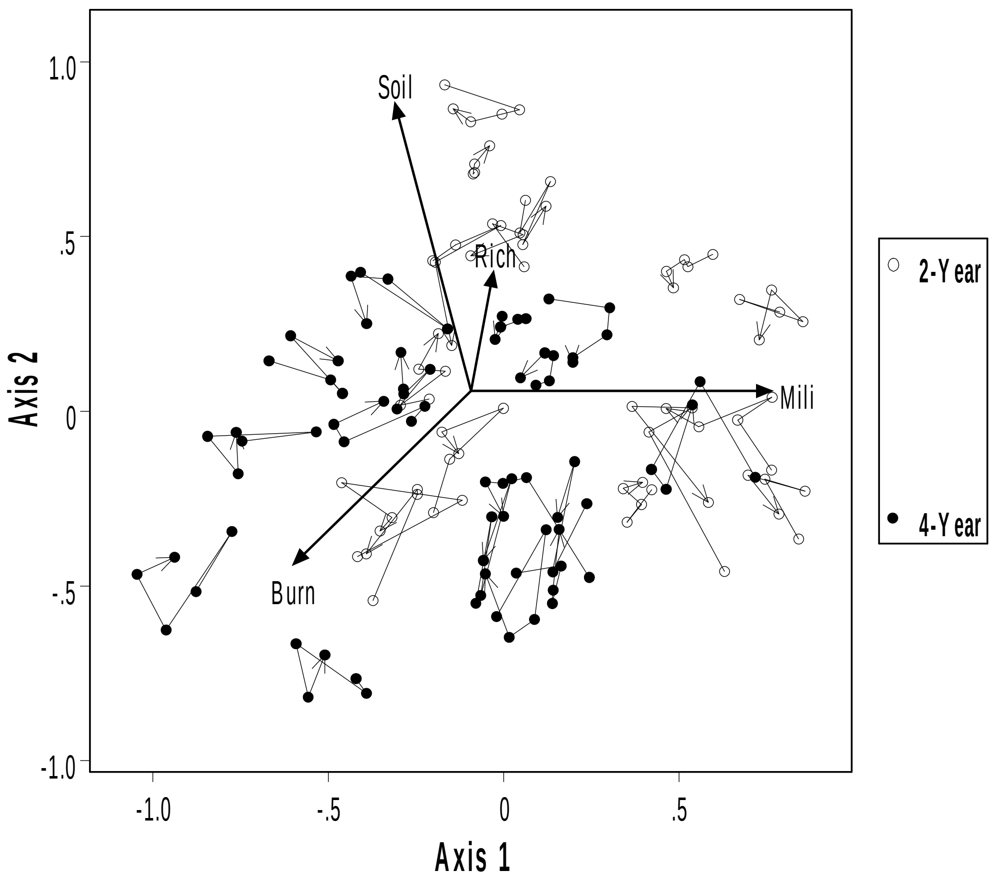


Figure 11. NMDS ordination of ground layer vegetation, annotated to show Fire Frequency. Points for a site are joined over years, with an arrow head pointing to the final year's point. Fitted vectors of maximum correlation are overlaid for Military Use (Mili), Soil Texture (Soil), Fire Frequency (Burn) and Richness (Rich).

vector for Fire Frequency is oblique to those for both Military Use and Soil Texture. This means that 4-yr fire sites (F4) tend to have vegetation similar to sites with a combination of sandy soils and light military use, while 2-yr fire sites (F2) tend to have vegetation similar to sites with a combination of clayey soils and heavy military use. ANOSIM using the data from all years finds a significant difference in community composition between F2 and F4 sites ($R=0.1426$, $p<0.0001$), but separate ANOSIM tests using the data for each sampling year show that this difference did not develop until 2002 (Table 7). The lack of a community difference in 2000 and 2001 demonstrates that the random-assignment of sites to fire treatments was successful. Community differences in 2002 through 2004 are presumably the result of the accelerated prescribed fire treatment (F2).

Indicator species analysis, using the combined data from 2002 through 2004, identified 43 species (mostly non-woody legumes, graminoids, and forbs) that are indicators of F2 sites and 15 species (mostly woody) that are characteristic of F4 sites (Table 10). Abundant (> 1 % relative abundance) indicator species in F2 sites include *Rhus copallina*, *Tephrosia virginiana*, *Andropogon* sp., *Chrysopsis gossypina*, and, notably, *Pteridium aquilinum*. *Pteridium* was a dominant ground layer species in longleaf-dominated sites in 2000 (Table 1). Abundant indicator species in F4 sites include *Vaccinium arboretum*, *Liquidambar styraciflua*, *Quercus falcata*, *Smilax* sp., and *Vitis* sp.

Species	**Growth Form**	**Fire Frequency**		***p***
		F2	**F4**	
Pteridium aquilinum	Fern	**46**	11	0.0075
Agave virginica	Forb	**11**	0	0.0239
Agrimonia sp.	Forb	**13**	0	0.0114
Aletris farinosa	Forb	**11**	0	0.0242
Ambrosia artemisiifolia	Forb	**20**	0	0.0279
Angelica venenosa	Forb	**18**	0	0.0024
Aster linariifolius	Forb	**31**	0	0.0003
Asteraceae sp1.	Forb	**68**	20	0.0005
Asteraceae sp2.	Forb	**37**	2	0.0011
Chrysopsis gossypina	Forb	**16**	0	0.0039
Chrysopsis mariana	Forb	**38**	13	0.0321
Cnidoscolus stimulosus	Forb	**40**	7	0.0319
Commelina virginica	Forb	**30**	1	0.0022
Eupatorium hyssopifolium	Forb	**45**	21	0.0495
Eupatorium rotundifolium	Forb	**26**	5	0.0432
Helianthemum rosmarinifolium	Forb	**13**	0	0.0186
Helianthus sp.	Forb	**48**	10	0.0497
Heterothica graminifolia	Forb	**69**	31	0.0226
Hieracium gronovii	Forb	**50**	2	0.0001
Lechia villosa	Forb	**18**	1	0.0249
Senecio sp.	Forb	**9**	0	0.0493
Silphium compositum	Forb	**29**	5	0.0345
Silphium dentatum	Forb	**16**	0	0.0033
Stipulicida setacea	Forb	**15**	0	0.0081
Vernonia angustifolia	Forb	**53**	21	0.0222
Andropogon sp.	Graminoid	**67**	33	0.0005

Carex sp.	Graminoid	**61**	37	0.0477
Digitaria sp.	Graminoid	**11**	0	0.0228
Juncus tenuis	Graminoid	**20**	1	0.0118
Paspalum sp.	Graminoid	**23**	2	0.044
Poaceae sp1.	Graminoid	**41**	16	0.0426
Tripascum dactyloides	Graminoid	**20**	0	0.0005
Cassia sp.	Legume	**62**	28	0.0096
Centrosema virginianum	Legume	**55**	17	0.0108
Clitoria mariana	Legume	**33**	6	0.0263
Crotalaria sp.	Legume	**14**	0	0.0243
Lespedeza sp.	Legume	**67**	31	0.0004
Schrankia microphylla	Legume	**26**	3	0.0206
Stylosanthes biflora	Legume	**52**	10	0.0102
Tephrosia spicata	Legume	**50**	8	0.0032
Tephrosia virgininana	Legume	**38**	3	0.0092
Rhus copallina	Shrub	**59**	39	0.0356
Quercus marilandica	Tree	**32**	7	0.039
Hexastylis arifolia	Forb	0	**15**	0.0119
Hypericum hypericoides	Forb	0	**14**	0.0376
Oxalis sp.	Forb	2	**19**	0.0429
Rosa sp.	Shrub	2	**18**	0.0425
Vaccinium arboreum	Shrub	34	**58**	0.0263
Vaccinium stamineum	Shrub	16	**77**	0.0001
Acer rubrum	Tree	2	**53**	0.0002
Aesculus pavia	Tree	0	**15**	0.0126
Ilex opaca	Tree	0	**27**	0.0003
Liquidambar styraciflua	Tree	18	**75**	0.0001
Quercus falcata	Tree	9	**79**	0.0001
Quercus nigra	Tree	21	**68**	0.0021
Parthenocissus quinquefolia	Vine	1	**34**	0.0022
Smilax sp.	Vine	26	**74**	0.0001
Vitis sp.	Vine	27	**67**	0.0003

Table 10. Results of Indicator Species Analysis between Fire Frequency treatments, using combined data from years 2002 through 2004. For more explanation, see caption of Table 8.

Overall, the vegetation analyses suggest the shorter, 2-yr fire interval caused the ground layer vegetation to become more similar to that of clayey sites with heavier military use; i.e., to be characterized by sandhills species and nonwoody legumes, graminoids, and forbs. To determine if shorter or longer fire intervals caused ground layer vegetation to become more or less like that of longleaf sites, we used analysis of dissimilarity to test differences in each year between the ground layers of longleaf stands and those of the combined other (pine-hardwood, shortleaf, loblolly) forest types in the combinations of soil texture, military use, and fire frequency. As illustrated in Fig. 12, clayey sites with lighter military use (F2MlC, F4MlC) differed initially from longleaf sites, and both 2-yr and 4-yr fire treatments became increasingly different through 2003. Sandy sites in the 4-yr fire treatment also had significantly different ground layer composition from longleaf sites by 2001 (yr 2), and they remained different through 2004. The results do not indicate the shorter, 2-yr fire interval caused dissimilar sites to become more similar to, or similar sites to diverge from, longleaf communities. The results do suggest that either 1) heavier military use or shorter fire frequency in clayey sites, or 2) shorter fire frequency in sandy sites can maintain ground layer composition similar to that of longleaf sites. Indicator species analysis was run for the 2003 ground layer data (i.e., the second year of the second fire interval in F2 sites and the fourth year of the of interval in F4 sites) between the group of longleaf sites plus the other sites that did not differ from them (Fig. 12) and the group of significantly different sites (Fig. 12). This analysis found 10 indicator taxa for longleaf+ communities and 8 taxa for the ‘different’ forest types (Table 11). Indicator taxa for the longleaf+ communities include *Pteridium aquilinum* and others that characterize 2-yr (F2) sites and clayey soil with both heavier and lighter military use. Within the context of the Fort Benning ecosystem restoration and management model (Fig. 8, 12), the 2-yr fire interval and

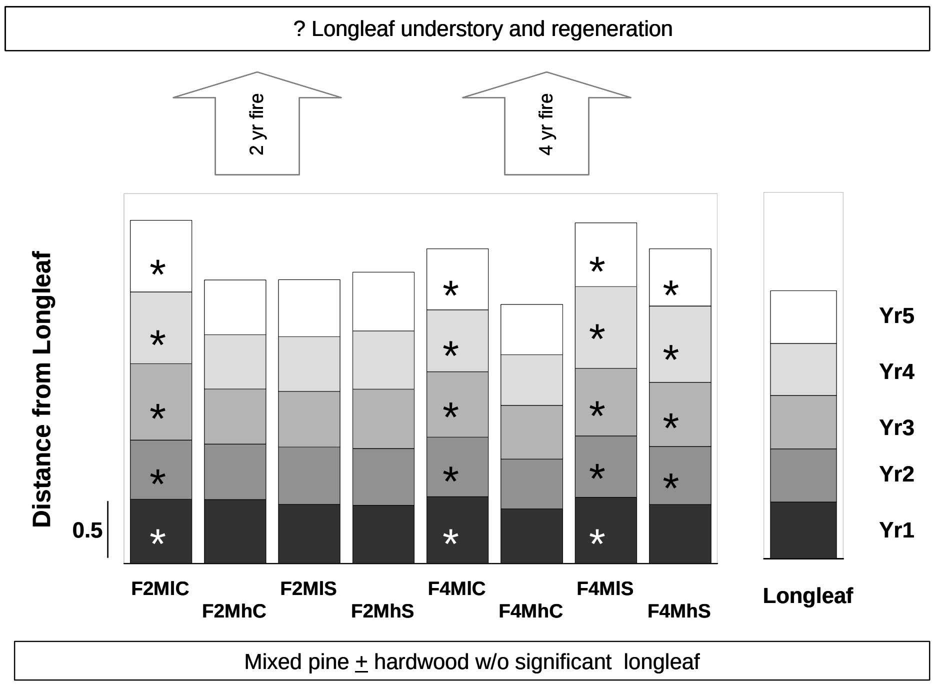


Figure 12. Boxes show mean ground layer vegetation distance (Bray-Curtis dissimilarity) in each year from 2000 (black box) to 2004 (white box) within longleaf-dominated sites (Longleaf) and between longleaf and the group of all other sites (pine-hardwood, shortleaf, loblolly) in each fire frequency (F2,4), military use (Ml,h) and soil texture (S,C) combination. An asterisk indicates significant differences from the ground layer communities of longleaf sites.

heavier military use in clayey sites or the 2-yr fire interval in sandy sites may maintain sites within the desired longleaf understory domain. In contrast, longer, 4-yr fire intervals in sandy sites or the combination of longer fire interval and lighter military use in clayey sites may cause sites to move away from the longleaf domain and lengthen the successional trajectory.

Species	Forest Type		*p*
	Longleaf	Combined other	
Pteridium aquilinum, F2	**58**	6	0.0097
Quercus stellata	**49**	0	0.0075
Tephrosia spicata, F2, C	**49**	8	0.045
Silphium compositum, F2	**49**	1	0.0069
Poaceae sp1, F2	**48**	5	0.0306
Chrysopsis mariana, F2, Mh, C	**46**	3	0.0352
Quercus marilandica, F2	**45**	1	0.0201
Rhynchosia tomentosa, Mh	**43**	0	0.0119
Callicarpa americana, Ml	**41**	0	0.0183
Viola spp.	**39**	1	0.0306
Quercus falcata, F4, S	20	**56**	0.0506
Myrica cerifera, Ml	14	**59**	0.0331
Ilex glabra, S	3	**36**	0.0436
Stylisma patens, Mh, S	1	**40**	0.0305
Hypericum sp.	0	**36**	0.0112
Desmodium sp2.	0	**29**	0.0267
Ilex opaca, F4, Mh, S	0	**29**	0.0295
Yucca filamentosa, S	0	**36**	0.0099

Table 11. Results of Indicator Species Analysis between the group of sites with ground layer composition similar to that of longleaf sites and the group of sites with significantly different ground layer composition (see Fig. 12). Ground layer data for 2003 were used. For more explanation, see caption of Table 8. Appended to each taxon name are the fire frequency (F2,4), military use (Ml,h), or soil texture (S,C) categories for which the taxon was a significant indicator.

Results from the study of legume and ground layer biomass responses to the 2-yr prescribed fire, which are summarized in a thesis "Groundcover carbon and nitrogen cycling and legume nitrogen inputs in a frequently burned mixed pine forest" by S. J. Drake (M. S. Thesis, University of Georgia), show an interaction between soil texture and prescribed fire. Ground layer biomass in the sampled mixed pine hardwood stands (85 g/m^2 in sandy sites – 106 g/m^2 in clayey sites) during the very dry summer of 2002 was intermediate to that reported for other southeastern forests. Total aboveground biomass did not differ with a 2-year or 4-year fire frequency or with soil texture (sandy vs. clayey soil). Grass aboveground biomass was lower on sandy than on clayey sites, but was higher relative to other plant groups in the 2-yr compared to 4-yr sites, which suggests a more pronounced response to fire in the sandy sites. Greater belowground biomass in sandy compared to clayey sites is consistent with the observation that some plants respond to nutrient or water stress by allocating a greater proportion of their biomass to belowground structures (Keyes and Grier, 1981).

The combined biomass of the six abundant harvested legumes was greater in clayey sites with a 2-year fire frequency (F2/clayey) and sandy sites with a 4-year fire frequency (F4/sandy). However, at the plot or community level (i.e., on an area basis), legume biomass was greater in F4/clayey and F2/sandy sites. This greater biomass offset greater activity (as measured by acetylene reduction), per-plant nodule mass, and per-plant biomass in F2/clayey sites and F4/sandy sites to lead to higher stand-level N fixation rates in 4-year/clayey sites and 2-year/sandy sites. However, it is not likely that the legumes contributed substantially to stand-level N inputs via litter. Although they had the greatest tissue C (%) and N (%) concentrations of the plant groups, and thus provide high-quality nitrogen-rich litter input to the ecosystem, legumes made up only 4 % of the total ground layer biomass. We conclude that frequent burning has not resulted in high levels of legume abundance and associated N inputs in the sampled stands.

The vegetation analyses enabled us to determine if a shorter, 2-yr or longer, 4-yr prescribed fire interval influenced ground layer composition, including legume biomass and activity; the successional trajectory; or transition to longleaf understory in sandy or clayey sites with lighter or heavier military use. To determine if fire interacts with soil texture or military use to influence longleaf regeneration, as desired in the ecological restoration plan for Fort Benning, we examined 1) density of natural regeneration and survival of marked, naturally-established pine and hardwood seedlings and sprouts from 2001 to 2002 (the year before and after the 2-yr prescribed fire treatment), and 2) density of longleaf (germinant through sapling stages) in 2004.

A total of 10,061 seedlings and sprouts, or 1.3 per m^2, were censused in 2001. Of these, only 31 were conclusively identified as longleaf; another 68 were identified as loblolly; the remaining 2,958 pine seedlings could not be identified to species. The longleaf seedlings were primarily in two sites. Many (11, or .04 per m^2) were in A15, which is dominated by longleaf and has a history of frequent fires; another group (8, or .03 per m^2) were in D16H, which has heavier military use and is classified as a shortleaf site, but has longleaf in the canopy. In 2002, only 2,986 (0.4 per m^2) seedlings and sprouts were present. Only five pine seedlings were identified as longleaf and only two as loblolly; the

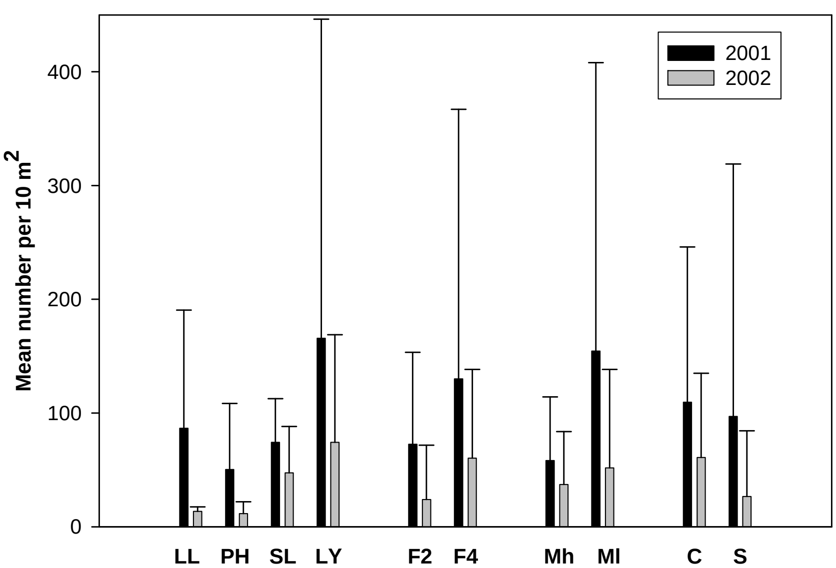


Figure 13. Mean density of pine (*P. palustris*, *P. taeda*, *P.* sp.) seedlings in forest types (Longleaf (LL), Pine-hardwood (PH), Shortleaf (SL), Loblolly (LY)), 2-yr (F2) and 4-yr (F4) fire categories, heavier (Mh) and lighter (Ml) military use sites, and sandy (S) and clayey (C) soil sites.

remaining 847 could not be identified to species. With all pine seedlings combined (Fig. 13), density in both years tended to be greatest in stands dominated by pine, the F4 fire treatment, sites in lighter military use, and clayey sites, although there were too few seedlings over all stands for a strong statistical test. In 2002, more than half (58 %) of all pine seedlings were concentrated in three sites: C1A (28 %), a loblolly site on sandy soil, with lighter military use and 4-yr fire frequency; Q3A (19 %), a loblolly site with clayey soil, lighter military use, and 4-yr fire frequency; and O10A (10 %), a longleaf site with sandy soil, lighter military use, and a 2-yr fire frequency.

With all species combined, seedlings and sprouts in longleaf stands had significantly higher mortality, and those in shortleaf stands lower mortality, than seedlings in mixed pine-hardwood or shortleaf stands (Fig. 14). Mortality was higher in 2-yr fire (F2) sites, which included the longleaf stands and were burned between the 2001 and 2002 surveys, than in 4-yr (F4) sites, and in clayey sites compared to sandy sites (Fig. 14). Over half (57 %) of marked pine seedlings (*P. palustris*, *P. taeda*, *P.* sp.) died between 2001 and 2002. Pine seedling mortality was strikingly higher (p = 0.0004) in longleaf stands (61.5 %) than in loblolly (9.8 %), shortleaf (3.5 %), or pine-hardwood (23.7 %) stands. Mortality was also higher (p = 0.0001) in 2-yr (26.6 %) compared to 4-yr (8.9 %) fire frequency.

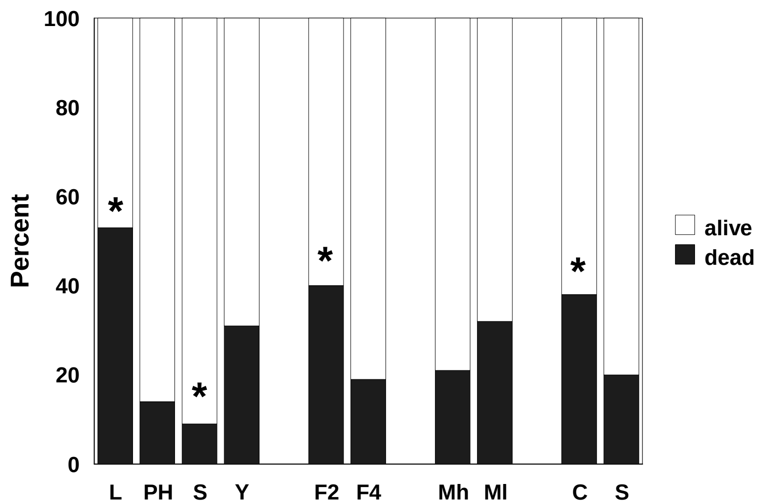


Figure 14. Percent of seedlings and sprouts marked in 2001 that were alive or dead in 2002 in each forest type (L, PH, S, Y), fire frequency category (F2, F4), military use category (Mh, Ml), and soil texture category (S, C).

In summer, 2004, after all sites were burned following both 2-yr fire (F2) intervals and one 4-yr fire interval (F4), longleaf regeneration (censused as germinants (pre-grass stage), grass stage, rocket stage, and saplings) was low over all sites. No germinants (pre-grass stage) were observed in any site (with 960 m^2 surveyed per site). With regeneration stages pooled, density varied from <1 to ca. 300 individuals per ha. Forest type was the strongest influence on longleaf regeneration. The number of grass (P<0.0005), rocket (P<0.0001), and sapling stage (P<0.0001) individuals was highest in longleaf stands (Fig. 15). Differences among fire intervals, soil texture categories, or military training categories were less pronounced, with insignificantly greater regeneration in clayey sites with lighter military training and a 2-yr fire interval (Fig. 15). Several measures of site condition were significantly related to the density of grass, rocket, or sapling individuals. The number of grass stage individuals in a stand increased with a) the number of historical fires (1980-2000; P=0.008), longer time since fire (P<0.0001), and the percent of sand in the soil (P=0.02); these conditions were common in longleaf stands. The number of rocket stage individuals decreased with increasing leaf area index (P<0.0001) and

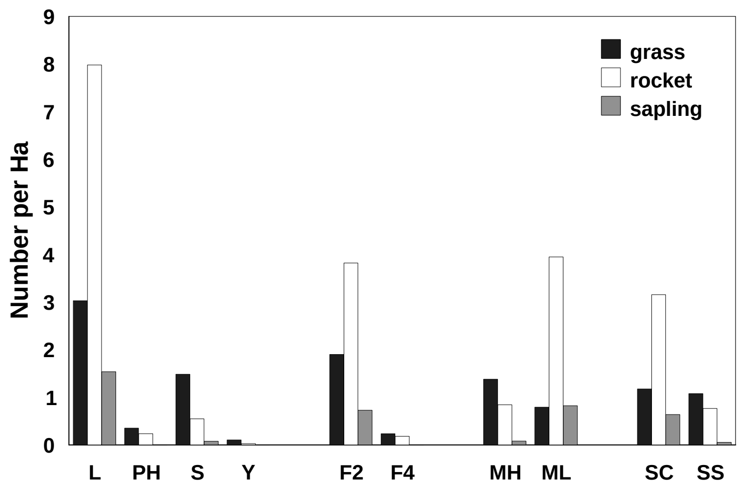


Figure 15. 2004 survey of longleaf regeneration

decreasing canopy openness (P<0.0001) as well as increasing abundance of disturbance features (P=0.02; see disturbance survey above). The number of rocket stage individuals increased with increasing number of historical fires (P=0.02). These conditions were common in longleaf and shortleaf stands that had experienced higher fire frequency and forest management for an open canopy, but lighter military use.

Collectively, the results indicate that longleaf regeneration is low over all the sampled sites. Greatest regeneration is in sites with pine canopy and existing longleaf seed trees. Although either 1) heavier military use or shorter fire frequency in clayey sites, or 2) shorter fire frequency in sandy sites can maintain ground layer composition similar to that of longleaf sites, these land uses do not promote longleaf regeneration sufficient to hasten transition to a longleaf pine forest because repeated frequent fires inhibit seedling establishment. If, however, seedling establishment limitation is overcome (e.g., by planting), management that maintains a relatively open canopy (prescribed fire, thinning) and low soil disturbance (lighter compared to heavier military training), can promote growth into grass, rocket, and sapling stages.

Results after four years: avian species as indicators

Results of the study of avian species as indicators of disturbance generated by land use at Fort Benning are summarized in “Avian response to forest management and military training activities at Ft. Benning, GA” by L. Duncan, J. Dilustro, and B. Collins, published in Georgia Journal of Science 62(2): 95-103. We found that abundances of individual bird species differed most often between land use category extremes. Early successional indigo buntings and northern bobwhites were more abundant in stands with heavier military training and most recently burned (F2Mh) than in stands with lighter military training and in their third growing season post-fire (F4Ml). In contrast to the early succession and pine grassland species, forest-dwelling red-eyed vireos were more abundant in F4Ml stands than in F2Mh stands. Tufted titmice, which have been suggested as potential indicators of fire exclusion, occurred less often in recently burned F2 sites than in F4 sits. Although these avian species may not discriminate finely over a landscape and region that reflects a long history of natural disturbances and intensive land use, examining the abundance of groups of species that use similar habitats (such as early successional and pine-grassland species) may be useful in defining disturbed habitats at Fort Benning. Our results suggest a more intensive study of avian abundance across Fort Benning that better defined distribution and population patterns would reveal that early successional and pine-grassland species are positively affected by management practices; conversely forest species and habitat generalists may utilize less disturbed areas.

Results after four years – soil

Soil CO_2 efflux: The results of the study of soil texture effects on soil CO_2 efflux in F4 (4-yr fire) sites from 2002-2003 are summarized in a paper "Moisture and soil texture effects on soil CO_2 efflux components in southeastern mixed pine forests" by J. Dilustro, B. Collins, L. Duncan and C. Crawford, published in Forest Ecology and Management 204:85-95. Over the two-year period, which included summer drought and a more typical rainfall year, the seasonal pattern and magnitude of soil CO_2 efflux were similar to southeastern pine plantations (Maier and Kress 2000, Coleman et al. 2000, Gough and Seiler 2004). The overall pattern of soil CO_2 efflux was related primarily to soil temperature, but we identified several soil quality parameters (soil A layer, soil organic layer mass) to be significantly related to the general pattern. In addition, soil texture influenced soil CO_2 efflux response to soil moisture. Soil CO_2 efflux was significantly related to soil moisture only in sandy sites when soil water content was above the wilting point threshold. Further, soil CO_2 efflux was suppressed in the sandy sites during the warm, dry September, 2003 sampling period (Table 12). There were no significant relationships between soil moisture and soil CO_2 efflux in the clayey sites over the range encountered during sampling.

		2003			
Sites	Component	April	June	Sept	Total
Clayey	Surface root exclusion	2.42	4.00	3.63	3.36 (0.10)
	Total soil CO_2 efflux	2.77	4.77	4.35	3.96 (0.15)
	Soil moisture (% vol)	16.99	20.21	9.26	15.49 (0.59)
	Surface root respiration	0.35	0.77	0.72	0.60
Sandy	Surface root exclusion	2.32	3.02	2.50	2.61 (0.10)
	Total soil CO_2 efflux	2.30	3.34	2.49	2.71 (0.13)
	Soil moisture (% vol)	8.00	6.79	2.79	5.86 (0.40)
	Surface root respiration	0	0.32	0	0.10

Table 12. Components of soil CO_2 efflux in clayey or sandy sites during the growing season, 2003. Shown are mean soil CO_2 efflux with surface roots excluded, total soil CO_2 efflux, surface root CO_2 efflux ($\mu mol\ m^{-2}\ s^{-1}$) and soil moisture (% volumetric). Only sites with both control and root exclusion treatments are shown (n=3). 2003 yearly total means and standard errors (SE) are shown.

The contribution of root respiration (R_r) to total soil CO_2 efflux during the growing season was estimated to be 10% (2002) and 4 % (2003) in the sandy stands, and 12.3 % (2002) and 15 % (2003) in the clayey stands. These estimates are lower than those reported for many forests (Hanson et al. 2000), perhaps as a result of our relatively shallow (10 cm) root exclusion treatments, which gave estimates based only on the surface root fraction. Results of the root ingrowth bags, which showed greater root production over a one-year period in sandy stands (Table 13), were not consistent with the lower R_r in these stands during the 2002 and 2003 growing seasons. Differences between the more integrated year-long root production sampling and the seasonal root respiration sampling likely contributed to this discrepancy.

Microbial biomass carbon (MBC) values (132-250 µg/g dry wt soil) measured in May, 2003, in eight stands (Table 13) were similar to those reported from other upland forest stands on Ft. Benning (100-300 µg/g dry wt soil; J. Zak unpublished data, 2004). Greater MBC in clayey compared to sandy sites potentially contributed to the greater total soil CO2 efflux in these stands. However, soil MBC pool size may or may not be well correlated with microbial activity and soil CO2 efflux (Wang et al 2003).

Variable	Sandy Stands	Clayey Stands
Soil Respiration 4/03	2.30 µmol m^{-2} s^{-1} (n=3)	2.77 µmol m^{-2} s^{-1}
Microbial Biomass Carbon* 5/2003	132.41 µg/g dry wt of soil	249.63 µg/g dry wt of soil
Fine root production* 6/2003	344.79 $g/m^2/yr$ (n=3)	265.97$g/m^2/yr$
Soil Temperature instantaneous 4/03	19.46 ^{o} C (n=3)	19.06 C

Table 13. Means of soil CO_2 efflux, microbial biomass, fine root production and instantaneous soil temp (top 10 cm) for the 2003 growing season. N= 4 per treatment except where noted. * = P<0.05

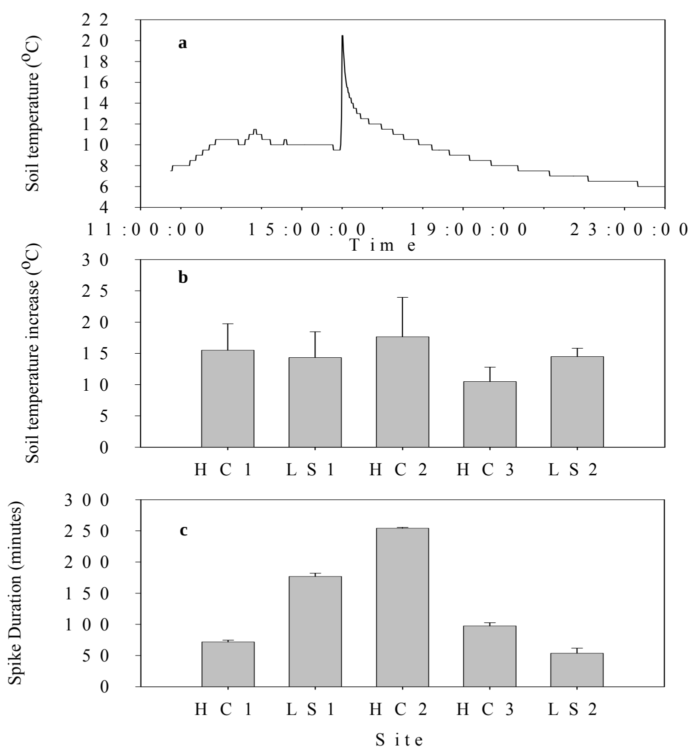


Figure 16. Soil temperature response to prescribed fire. a) Representative fire – 10cm depth; b) Mean temperature increase = Tspike –Tprefire; c) Time to return to prefire

In combination, results of the CO_2 efflux study suggest that variation in soil texture and associated abiotic and biotic conditions can influence soil CO_2 flux in upland forests at Fort Benning. In addition, management activities that alter soil carbon pools, temperature, and soil moisture influence activity of soil CO_2 efflux components.

Response to fire: The prescribed fires in 2002 had various effects on the soil. Figure 16a shows a typical soil temperature response. Temperature loggers were successfully deployed and retrieved in five stands. The fires were fairly uniform, with good coverage within each stand. Among the stands, maximum soil temperatures during the fire ranged from 15 °C to 43 °C. Temperature increases, normalized by subtracting the maximum pre-fire temperature from the maximum elevated temperature (T_{max}) at each sensor location, did not differ among the stands ($F=0.41$, $P=0.79$; Fig. 16b). The duration of elevated temperature varied among stands ($F=275.48$, $P<0.0001$); the stand with the longest elevated temperature, D16C, was the only site in which the fire was ignited before noon (Fig. 16c). Fires were ignited in early afternoon in the other four stands.

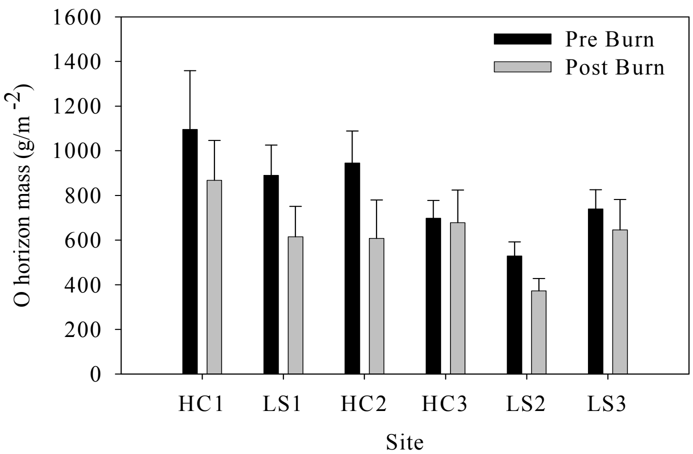
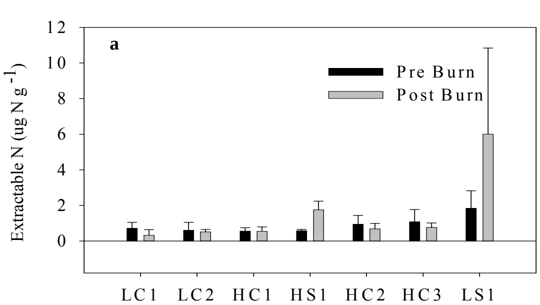


Figure 17. O horizon mass before and after

Mass of the pooled organic layer was compared before and after fire in six stands (Fig. 17). The prescribed fires led to a significant ($F=4.98$, $P<0.0284$) reduction in organic layer dry mass; the post-fire organic layer ranged from 2% to 36% pre-burn mass (Fig 17). Organic layer response to fire also differed among stands ($F=2.83$, $P<0.0206$).

Available soil N, measured as extractable N (five stands) and total soil N (%N) (seven stands), showed little response to prescribed fire. Although change in mineral soil extractible total N following fire ranged from a 54% decline to a 327% increase among stands (Fig. 18a), variability was high and these differences were not significant ($F=1.79$, $P<0.1221$). All values were low (<6 µg N g^{-1} soil), and fire did not result in a significant change in extractable mineral soil N ($F=0.79$, $P<0.3798$). There also was little change in percent total N after fire in most stands (Fig. 3b); two stands experienced larger losses of total N and no stand showed a large accumulation (Fig. 18b). The total N and $\delta^{15}N$ data were not analyzed statistically due to a lack of replicated samples. $\delta^{15}N$ values generally increased with fire (Fig 18c). There was a general shift in soil N isotopic composition with enrichment observed after the fires.



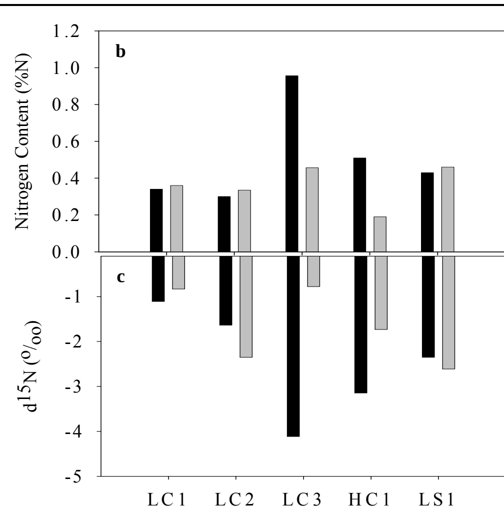


Figure 18. Immediate extractable a) total ($NO_3 + NH_4$) soil N, b) mineral soil %N, and c) δ15N, pre and post prescribed fires.

Longer term, seasonal evaluation of fire effects on the soil was only performed for the organic layer mass and extractable N components. Organic layer mass, collected from eight clayey and seven sandy soil stands in the growing season prior and subsequent to the prescribed fires, was significantly reduced after the fires (F=18.08, P<0.0001; Fig. 19a), but the reduction did not differ between soil texture groups (F=2.44, P<0.1197). Total extractable N was significantly greater in the growing season following prescribed fire (F=22.92, P<0.0001; Fig. 19b), and varied between stand soil texture groups (F=4.41, P<0.0378) with greater extractable N on the clayey stands.

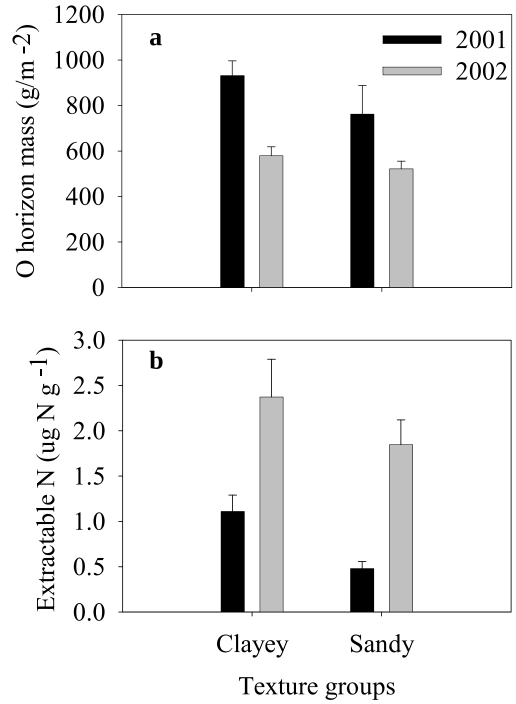


Figure 19. 2001 (prior growing season) and 2002 (subsequent growing season) a) organic layer mass and b) extractable total (NO_3 + NH_4) soil N for sandy (N=7) stands and clayey (N=8) stands.

Mineral soil was analyzed for nitrogen content in all 32 stands in 2001 and 2003. Soil nitrogen content had a significant soil*use interaction (P<0.0001) and year sampled was not significant (Fig. 20). The greater soil nitrogen on the light use clay sites reflects the greater tree density on these sites. The absence of a change in soil nitrogen concentration over this period is expected due to the slow response time of mineral soil nitrogen concentration to any ecosystem alteration. Soil responses to prescribed fire over the study period indicate low intensity burns resulting in reductions in soil organic layers and small but variable alteration in inorganic soil nitrogen.

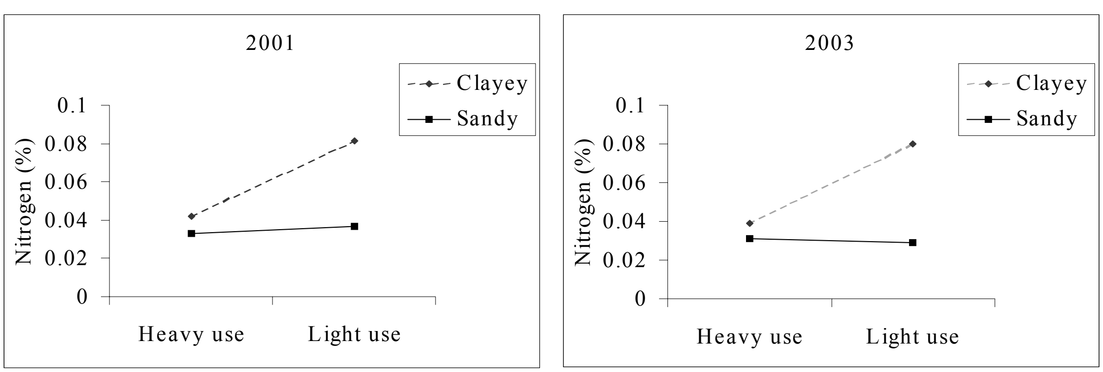


Figure 20. Mineral soil nitrogen a) 2001 b) 2003 post prescribed burns for both soil texture groups and use intensity

Conclusions

Over the longer term (decades), military training and frequent fire have interacted with soil texture to influence forest canopy and ground layer composition, and soil conditions, at Fort Benning. Over the four-year term of our research, fire at two year intervals (on sandy sites), or frequent fire combined with heavier military use (on clayey sites), can cause convergence toward 'sandhills' ground layer vegetation dominated by more xeric species, graminoids, and legumes, but these land uses are not sufficient to cause initially dissimilar sites to shift (cross a threshold) to longleaf pine understory. Management to restore longleaf pine forests must overcome recruitment limitations and may be inhibited by frequent fire; recruitment of longleaf was nonexistent to low over all sites and seedlings/sprouts of all species were reduced by prescribed fire. If recruitment limitation is overcome, management that maintains a relatively open canopy and low soil disturbance can promote longleaf pine growth into grass, rocket, and sapling stages and may facilitate restoration of longleaf pine ecosystem as conceptualized in the Fort Benning ecological restoration model.

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Conclusions

Baseline surveys conducted in 2000 and 2001 revealed that military training and frequent fire have, over the longer term (decades), interacted with soil texture to influence forest canopy and ground layer composition, and soil conditions, at Fort Benning.

- The survey of disturbance features revealed that land use or natural disturbance features occupied from 7% to 50% of the area sampled in each site. Road-like features, including active and remnant trails, roads, and vehicle tracks or trails, were, collectively, the most frequent and abundant disturbance. Disturbance features were most abundant in clayey sites in heavy military use areas.
- Differences in soil properties among the 32 upland forest stands were related to soil texture and military land use intensity. Results suggest organic layers in sandy compared to clayey sites could immobilize nitrogen through relatively slow rates of decomposition and nitrogen release to the mineral soil, but mineralization processes in the mineral soil could enhance nitrogen availability, especially in land compartments with heavier military training. In clayey sites, greater organic layer mass, particularly in sites with lighter military use, favors faster decomposition, but the lower nitrogen availability observed in the field on the heavier use sites suggests mineralized nitrogen can be bound by fine soil particles.
- Ordination revealed a strong effect of military training on initial (2000, 2001) canopy and ground layer composition. The canopy tree ordination also reflected the proportion of pine, particularly longleaf pine. We distinguished four stand types, based on the dominant canopy trees: longleaf pine stands, shortleaf stands, mixed pine hardwood stands, and loblolly stands. Although differences were less pronounced than in the canopy, ground layer vegetation also reflected the canopy dominant. Pine-hardwood and longleaf stands had different ground layer composition. *Andropogon* sp., primarily broomsedge, *A. virginicus*, *Pityopsis*, and sweetgum (*Liquidambar*) seedlings were abundant in multiple canopy types. Pine-hardwood forests had abundant *Vitis* sp, while bracken fern (*Pteridium aquilinum*) was abundant in longleaf stands. The abundance of legumes and grasses was higher in the longleaf stands than in the other forest types. Over all forests types, 70 % pine canopy appears to be a threshold for ground layer vegetation with abundant grasses and legumes.

Over the shorter term of our research (4 yr) land use had measurable, but less pronounced effects on vegetation and soil.

- Vegetation analyses after two, 2-yr fire cycles and one, 4-yr cycle revealed the shorter, 2-yr fire interval caused the ground layer vegetation to become more similar to that of clayey sites with heavier military use; i.e., to be characterized by more xeric sandhills species and nonwoody legumes, graminoids, and forbs.
- Prescribed burning at Ft Benning reduces the soil organic layer, a largely immobilizing nitrogen pool in these systems. The removal doesn't represent a reduction in immediate nitrogen availability, but rather a reduction in total N pool. The longer-term consequences of this removal are not well understood and a long-term monitoring plan should address this to ensure the system doesn't trend toward nitrogen deficiency. Presently, on most sites, nitrogen fixation does not supply sufficient fixed nitrogen to offset these organic layer nitrogen losses.
- Comparisons between longleaf and initially dissimilar sites revealed either 1) heavier military use or shorter fire frequency in clayey sites, or 2) shorter fire frequency in sandy sites

can maintain ground layer composition similar to that of longleaf sites. These results partially support our hypothesis that the magnitude of ecosystem response to fire and military training disturbance would be less, and the transition to pine-dominated forest faster, for sites on sandy soils; shorter fire frequency alone can maintain longleaf ground layer composition on sandy sites, but both shorter fire frequency and heavier military training may be needed in clayey sites.

- Comparisons between longleaf and initially dissimilar sites revealed the shorter, 2-yr fire interval was not sufficient to shift ground layer composition to the longleaf domain. Shorter fire interval did not cause sites that were initially different to become more like, or initially similar sites to diverge from, longleaf communities.

Within the context of Fort Benning ecosystem management model and SREL's research design, the longer, 4-yr fire intervals in sandy sites or the combination of longer fire interval and lighter military use in clayey sites may cause sites to move away from the longleaf domain and lengthen the successional trajectory. In contrast, a 2-yr fire interval and heavier military use in clayey sites or the 2-yr fire interval in sandy sites may maintain sites within the desired longleaf understory domain. However, in sampled stands the more frequent burning did not result in high levels of legume abundance and associated N inputs, which could offset nitrogen losses due to fire. Further, more frequent burning did not promote longleaf regeneration sufficient to hasten transition to a longleaf pine forest. Thus, despite promoting desirable understory composition, more frequent fire may inhibit regeneration. These results only partially support out hypothesis that the more open environment generated by heavier training and frequent fire could promote regeneration of species typical of pine ecosystems, and hasten transition to a longleaf pine forest. If seedling establishment limitation is overcome, e.g., by planting, management that maintains a relatively open canopy (prescribed fire, thinning) and low soil disturbance (lighter compared to heavier military training), can promote growth into grass, rocket, and sapling stages. In summer, 2004, after all sites were burned following both 2-yr fire intervals and one 4-yr fire interval, the number of grass stage individuals in a stand increased with the number of historical fires (1980-2000), longer time since fire, and the percent of sand in the soil; the number of rocket stage individuals increased with increasing number of historical fires. These conditions were common in longleaf and shortleaf stands that had experienced higher fire frequency and forest management for an open canopy, but lighter military use.

We conclude that management to restore longleaf pine forests must overcome recruitment limitations and may be inhibited by frequent fire. In addition, restoration of a more legume dense groundcover would aid in nitrogen supply to these forests. If recruitment limitation is overcome, management that maintains a relatively open canopy and low soil disturbance can promote longleaf pine growth into grass, rocket, and sapling stages and may facilitate restoration of longleaf pine ecosystem as conceptualized in the Fort Benning ecological restoration model.

Appendix A

List of Technical Publications

Papers

Dilustro J.J., Collins B., L. Duncan and R. Sharitz. 2002. Soil Texture, land use intensity, and vegetation of Ft Benning upland forest sites. Journal of the Torrey Botanical Society 129(4):280-297

Collins, B. 2002. Symposium: regional partnerships for ecosystem research and management. SE Biology 49(4):372-378.

Duncan, L.K., J.J. Dilustro and B.S. Collins. 2004. Avian response to forest management and military training activities at Ft. Benning, GA. Georgia Journal of Science 62(2): 95-103.

Dilustro, J.J., B. Collins, L. Duncan and C. Crawford. 2005. Moisture and soil texture effects on soil CO_2 efflux components in southeastern mixed pine forests. Forest Ecology and Management 204:85-95.

Collins, B., R. Sharitz, K. Madden, and J. Dilustro. In press. Comparison of sandhills and mixed pine hardwood communities at Fort Benning, Georgia. Southeastern Naturalist.

Drake, S. J. J. Dilustro, R. R. Sharitz, and B. S. Collins. In press. Ground layer carbon and nitrogen cycling and legume nitrogen inputs in a frequently burned mixed pine forest. American Journal of Botany.

Theses

Drake, S. J. 2004. Groundcover carbon and nitrogen cycling and legume nitrogen inputs in a frequently burned mixed pine forest. M. S. Thesis, University of Georgia.

Presentations

Dilustro, J., B. Collins, and L. Duncan. Soil nitrogen availability in mixed pine forests of varying management, military use and soil texture. Soil Science Society of America meeting, November, 2004

Dilustro, J., B. Collins, L. Duncan, and C. Crawford. Soil respiration, microbial biomass, and fine root production in forests of varying soil texture. ESA meeting, Portland, OR, August, 2004.

Drake, S., J. Dilustro, B. Collins, and R. Sharitz. Groundcover carbon and nitrogen cycling in a frequently burned mixed pine forest. ESA meeting, Portland, OR, August, 2004.

Dilustro, J., B. Collins, L. Duncan, and C. Crawford. Soil respiration and fine root production in southeastern mixed pine forests of varying soil texture. ASB meeting, Memphis, TN, April, 2004

Collins, B. Land use effects on vegetation and nitrogen cycling at Fort Benning, GA. Drexel University, January, 2004.

Collins, B., J. Dilustro, L. Duncan, and R. Sharitz. 2003. Land use and land management effects on soil nitrogen cycling in upland forests at Fort Benning. SERDP Partners in Environmental Technology Technical Symposium, Washington, DC, December. (poster)

Crawford, C. B., J. J. Dilustro, and B. S. Collins, and L. Duncan 2003. Soil response to prescribed fire in mixed pine-hardwood forests at Ft. Benning, GA. Ecological Society of America annual meeting, Savannah, GA. August.

Dilustro, J. J., Beverly S. Collins, and Lisa K. Duncan. 2003. Soil nitrogen cycling in mixed forests of varying soil texture at Fort Benning, Georgia. Ecological Society of America annual meeting, Savannah, GA. August.

Drake, S. J., R. R. Sharitz, J. J. Dilustro, and B. S. Collins. 2003. A model for predicting C and N transformations and annual net primary productivity under differing burn frequencies in a southeastern mixed pine-hardwood forest. Ecological Society of America annual meeting, Savannah, GA. August.

Duncan, Lisa K., John J. Dilustro, and Beverly S. Collins. 2003. Avian response to forest management and military training at Fort Benning, Georgia. Ecological Society of America annual meeting, Savannah, GA. August.

Collins, B., J. Dilustro, and L. Duncan. 2003. Thresholds of disturbance and dynamics of mixed pine-hardwood forests at Fort Benning, GA. SE Biology 50:150.

Drake, S. J., R. R. Sharitz, J. D. Dilustro, and B. Collins. 2003. Aboveground peak biomass and groundcover plants in a mixed pine forest on sites with differing soil textures and burn frequencies. SE Biology 50:191.

Dilustro, J. J., B. S. Collins, and L. Duncan. 2003. Short-term response of soil to prescribed fire in mixed pine forests on Ft. Benning, Georgia. SE Biology 50:191.

Collins, B., J. Dilustro, and L. Duncan. 2002. Thresholds of disturbance and adaptive forest management. Natural Areas Conference, Asheville, NC, October. (presentation)

Collins, B. and J. Dilustro. 2002. What's going on at Fort Benning? SREL, November (presentation)

Collins, B., J. Dilustro, L. Duncan, and R. Sharitz. 2002. Thresholds of land use in upland forests at Fort Benning. SERDP Partners in Environmental Technology Technical Symposium, Washington, DC, December. (poster)

Dilustro, J. J., B. S. Collins, L. K. Duncan and R.R. Sharitz. 2002. Soil texture, nitrogen mineralization and vegetation of Fort Benning upland forest sites. ESA Meeting. Tucson, Arizona. August.

Dilustro, J. J., B.S. Collins, L.K. Duncan and R. R. Sharitz. 2002. Soil texture, land use intensity, and vegetation of Fort Benning upland forest sites. ASB Meeting. Boone, North Carolina, April. Southeastern Biology 49:160.

Collins, Beverly. 2002. Symposium: A regional perspective – partnerships for ecosystem research and management in the Southeast. ASB Meeting, Boone, North Carolina, April. Southeastern Biology 49:213.

Collins B., J.J. Dilustro, L. Duncan and R. Sharitz Soil texture, land use intensity, and vegetation of Fort Benning sandhills sites. 2001. SERDP Partners in Environmental Technology Technical Symposium and Workshop. Washington D.C.

Dilustro J, B. Collins, .L Duncan, R. Sharitz, J. Vaun McArthur, C. Romanek, J. Seaman. 2001. Land management and soil composition effects on vegetation and nitrogen dynamics in Ft Benning, Georgia. ESA Meeting. Madison, Wisconsin.

Dilustro J, B. Collins, .L Duncan, R. Sharitz, J. Vaun Mcarthur, C. Romanek, J. Seaman. 2001. Thresholds of Disturbance: Land management effects on vegetation and nitrogen dynamics. ASB Meeting. New Orleans, LA. (ASB Bull. 48:183)